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EDITORIAL

A Ciência é percebida sob vários enfoques.

Segundo o poeta grego da atualidade Alexandre Panagulis — “A ciência não existe, a ciência é uma opinião. E não demonstra coisíssima alguma, e muito menos a vida e a morte”.

Sob o nosso ponto de vista de educadora de Saúde Pública, a Ciência é resultante do esforço de algumas pessoas, dentro de suas limitações humanas, em busca da verdade, em busca da coerência, em busca de ser e do ser e dentro da filosofia da ciência a busca da *razão* da vida e da morte.

Este número de Memórias é dedicado a uma dessas pessoas, Dr. Alphonse Richard Hoge que na sua especialidade: — a busca da verdade científica em relação aos animais peçonhentos — dedicou toda sua vida na pesquisa desta área específica.

Embora a tendência atual seja a de formação de grupos multiprofissionais definindo uma metodologia científica, visando a interdisciplinariedade, justifica-se um número do periódico “Memórias do Instituto Butantan” dentro de uma só especialidade, uma vez que este volume reúne os trabalhos científicos apresentados em 1981 no 1.º *Simpósio Internacional sobre Serpentes em Geral e Artrópodes Peçonhentos*, organizado e coordenado pelo Dr. Alphonse Richard Hoge.

Após o Simpósio, realizado por ocasião da comemoração dos 80 anos da Fundação do Instituto Butantan, este cientista recolheu os trabalhos apresentados e solicitou a esta Comissão Editorial que fossem publicados nas suas formas originais.

Dr. Alphonse Richard Hoge faleceu em 25-12-82, deixando, entre outros, mais este legado aos estudos sobre animais peçonhentos desenvolvidos no Instituto Butantan.

ROSA PAVONE PIMONT

Presidente da Comissão Editorial
das Memórias do Instituto Butantan

Diretora da Divisão de Extensão Cultural



SciELO



ALPHONSE RICHARD HOGE
(1912-1982)



HOMENAGEM PÓSTUMA
ALPHONSE RICHARD HOGE
(1912-1982)

EMINENTE HERPETÓLOGO BRASILEIRO

Jesus Carlos MACHADO *

Designado pela Comissão Editorial das Memórias do Instituto Butantan, para escrever esta homenagem póstuma ao eminente pesquisador científico, Herpetólogo, Alphonse Richard Hoge, falecido aos 25 de dezembro de 1982, sentimo-nos como poucas vezes honrados por uma missão.

Julgamos que ao lado da fria relação dos seus trabalhos científicos adiante enumerados e do sumário do seu currículo fornecido pela sua esposa e colaboradora Alma R. Hoge, acreditamos ser extremamente adequado se tentarmos compor inicialmente a sua figura humana.

A sua pessoa, pela forma como desenvolvia o temário científico em que atuava — a herpetologia — confundia-se harmoniosamente com o próprio Instituto Butantan. Seu porte altivo e imperial, a lhanza incomum com que recebia indistintamente desde Reis, Príncipes, Chefes de Estado ou simples fornecedores de cobras e outros visitantes menos titulados, davam ao próprio Instituto Butantan um nível extremamente difícil de ser recomposto. As línguas que dominava desde o português, inglês, francês, alemão e mesmo o flamengo e africâner e outros que se fazia compreender, permitiam não só completar maravilhosamente sua formação científica pelo relacionamento e conhecimento mais profundos como impressionar favoravelmente aos que ele recebia gentilmente e com extrema boa vontade em seu laboratório. Sua preocupação pela Biologia e pela própria natureza transcendia o comum e recordo-me das longas conversas nas quais demonstrava sua alta cultura e elevado humanismo.

Os 36 anos de atividades no Instituto Butantan, tendo nele sua residência, permitiram que vivesse intensamente todos os seus problemas, não somente aqueles afetos à Divisão de Biologia que dirigiu desde 1969 até sua aposentadoria em Setembro de 1982, mas também todos os demais.

Seu cabedal científico era sólido e reconhecido internacionalmente, merecendo por isso condecorações (Medalha ao Mérito "Santos Dumont"; Medalha CNPq "Homenagem por contribuições técnicas e pesquisas" — 30.º Aniversário de Fundação — e Medalha permanente "Instituto Butantan") e convites para ser membro da Academia Real de Ciências d'Alem Mar (Bélgica) e Academia de Ciências do Estado de São Paulo. A lista de Instituições em que era Pesquisador Associado (Research Associate de "Duke University" — N. Car. USA; Research Associate "University of Michigan" — Ann Harbor Mi. USA; Research Associate "Smithsonian

* Diretor Técnico da Divisão de Patologia do Instituto Butantan.

Institution" United States N. Museum of Natural History; Washington D.C. USA; Investigador Associado da Seção de Herpetologia do Museu de Ciências Naturales de Caracas — Venezuela), as Sociedades de que era membro (Membro Fundador da Sociedade Brasileira para o Progresso da Ciência (SBPC); Membro Eleito da "The Society of the Sigma XI Devoted to the promotion of research in Science. Durham, North Carolina USA — 15-5-63, Duke University Chapter; "Dodonea Koninklyk Naturwetenschappelyk Genotschap, Gent, Bélgica, em reconhecimento às contribuições à Fauna ofiológica Neotrópica — Sócio honorário; Correspondente "Senckenbergische Naturforschende Gesellschaft" — Frankfurt a/Main, Alemanha; Correspondente do "Museum National d'Histoire Naturelle" — Paris, France; "Investigador (Ad Honoren)" da Seção de Herpetologia do Museu de Ciências Naturales, Conselho Nacional de Cultura — CONAC — Venezuela; "Snake Specialist Group" of the International Union for the Conservation of Nature Species Survival Commission — Madras, South India) demonstram sua sólida cultura científica especializada e seu excelente relacionamento internacional.

Demonstrou sempre profundo interesse pelos problemas da Ciência e preocupação pelos cientistas, sendo membro fundador da Sociedade Brasileira para o Progresso da Ciência e Conselheiro do movimento de Incentivo à volta dos Cientistas Brasileiros do Exterior ao Brasil.

No Instituto Butantan participou ativamente dos seus órgãos Colegiados tais como o Conselho Superior, quer como membro nato ou indicado pelo Secretário da Saúde; compôs o Fundo de Pesquisas, o Conselho de Pesquisas e foi membro da Comissão Editorial das Memórias do Instituto Butantan. Foi também Diretor-Substituto.

Participou ainda de numerosos grupos de trabalho e Comissões Especiais onde sempre demonstrou seu alto grau de bom senso e elevada qualificação técnica.

Os serviços prestados à comunidade fizeram-lhe merecedor dos Diplomas de Solidariedade Humana e Serviços Relevantes da FAB.

Enfim, foram 36 anos de atividades voltadas para a Instituição científica que o acolheu, atividades essas da mais alta qualificação técnico-científica emolduradas pela sua altiva figura humana, numa simbiose dificilmente encontrada e que envaideceram remarcadamente o Instituto Butantan.



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1.º SIMPÓSIO INTERNACIONAL
SOBRE
SERPENTES EM GERAL
E
ARTRÓPODES PEÇONHENTOS

INSTITUTO BUTANTAN
16 a 18 de novembro de 1981

COORDENAÇÃO
Alphonse Richard Hoge

Sob os auspícios do Governo do Estado de São Paulo e Conselho Nacional
de Desenvolvimento Científico e Tecnológico.





ANIMAUX VENIMEUX DE MADAGASCAR

Edouard Raoul BRYGOO *

Au XIX^{ème} siècle, la mauvaise réputation de Madagascar, parmi les Européens, reposait sur leur crainte des "fièvres", particulièrement redoutables pour le nouveau débarqué et nombre de naturalistes payèrent de leur vie la curiosité et l'audace qui les poussaient à découvrir un monde nouveau.

En contrepartie, très vite, s'accrédita l'idée que la Grande Ile n'avait pas d'animaux venimeux. De fait, ils y sont beaucoup plus rares que dans la plupart des pays tropicaux. Nous allons rapidement les passer en revue, traitant d'abord des invertébrés terrestres puis de la faune marine avant de nous étendre plus longuement sur les Ophidiens.

Invertébrés terrestres venimeux

Parmi les arthropodes, si l'on exclut les accidents possibles dus aux piqures d'hyménoptères qui ne sont pas plus agréables là qu'ailleurs il faut dire un mot des Araignées et des Scorpions.

a) Les Araignées.

La Grande Ile partage avec l'Europe et la Nouvelle Zélande le privilège d'avoir l'une des trois *Latrodectes* extra-américaines. Cette Theridiidé est bien connue des Malgaches. Selon Flacourt on la désignait sous le nom de "Vancoho", de fait le nom vernaculaire le plus utilisé aujourd'hui est "menavodi", ou "à cul rouge", en raison des deux taches rouges à la partie supérieure de l'abdomen, dont l'une à l'extrémité, taches qui tranchent sur la couleur générale noire encore qu'entre les deux taches rouges puissent s'observer trois séries de trois points blancs. Ce nom vernaculaire a servi à Vonson pour nommer l'araignée: *Latrodectes menavodi*. Un autre nom vernaculaire parfois utilisé est celui de "Tara-tra". Elle vit près du sol ou dans le sol, dans des lieux humides, à proximité ou sur des troncs d'arbres morts et décomposés. Elle ne doit pas être aussi dangereuse que son homologue sud-américaine, *L. mactans*, la trop célèbre veuve noire, car ayant dépouillé la littérature médicale malgache des origines à 1967, je n'y ai trouvé que 16 références traitant de cette araignée et des accidents d'aranéisme consécutifs à sa morsure,

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aucune ne rapporte de cas mortel. De son côté, Decary, en 28 ans de séjour, n'avait pas eu l'occasion de constater un cas certain de mort dû à cette araignée. Lavauden avait, en 1932, procédé à quelques expériences avec son venin, mais, à ma connaissance, il n'a plus été étudié depuis.

Madagascar compte plusieurs mygales de petite taille et divers araignées que la tradition populaire accuse de différents méfaits mais sans données positives pour étayer ces accusations. C'est en particulier le cas d'espèces du genre *Thomisus* qui, avec leur allure de crabe, ont la réputation d'être extrêmement dangereuses pour l'homme et le bétail; elles portent le nom local de "Foka".

b) Les Scorpions.

Depuis les travaux synthétiques de L. Fage, les Scorpions malgaches ont fait l'objet de récoltes et d'études suivies par J. Millot et M. Vachon. La meilleure revue est sans doute celle qu'en donnait en 1972 Roland Legendre (1). Quatorze espèces se répartissent en sept genres et deux familles, deux ne sont pas endémiques et appartiennent l'un à la faune cosmopolite, l'autre à celle d'Afrique du Sud. Les douze espèces endémiques font parties de cinq genres. Deux de ceux-ci sont endémiques: *Heteroscorpion* (Scorpionidae, Ischnurinae) et *Grosphus* (Buthidae, Buthinae). Les huit espèces de ce dernier, le seul genre plurispécifique, se répartissent les différentes zones biogéographiques de l'île. Ils sont en général de petite taille, vivent aussi bien en région forestière qu'en savane et portent les noms locaux de "Hetsé" ou de "Maingoka". Leur piqûre peut-être fort douloureuse mais elle ne doit pas être particulièrement dangereuse *quo ad vitam*, du moins je n'ai trouvé qu'une seule référence signalant un cas de piqûre par scorpion, ce qui, comparé aux seize concernant la *Latrodectes menavodi*, permet d'apprécier l'importance relative de ces arthropodes pour le médecin.

Animaux venimeux marins.

Les côtes et récifs de Madagascar sont fréquentés par des *Pterois*, poissons que les pêcheurs malgaches nomment "Lafa" et évitent avec soins. Mais chaque année ils provoquent des accidents sérieux chez les baigneurs et chasseurs sous-marins inexpérimentés, attirés par une splendide livrée bigarrée, aux nageoires longues et flottantes comme celles des poissons japonais.

Plus intéressante, car d'acquisition relativement récente, est la notion du danger dû aux mollusques du genre *Conus*.

Les Cônes, mollusques venimeux.

L'importance du danger que représentent pour l'homme les Cônes s'est considérablement accru au cours des dernières décades du fait de l'intérêt grandissant que leur portent les amateurs de coquilles. L'ouverture de Madagascar au tourisme international amène sur ses côtes nombre de collectionneurs et de collecteurs tandis que l'augmentation de

(1) Les Arachnides de Madagascar in *Biogeography and Ecology in Madagascar*, Battistini et Richard-Vindart éd., Junk publ. 1972 : 427-457.

la demande entraîne les populations locales à s'intéresser au ramassage de mollusques qu'autrefois elles négligeaient, d'où augmentation des occasions de contact entre les hommes et les mollusques et accroissement des risques d'envenimation.

L'Institut Pasteur de Madagascar a fait de l'étude du venin des cônes l'un de ses thèmes de recherches depuis 1971. Il a apporté les contributions nouvelles suivantes :

- mise en évidence, pour la première fois, de la toxicité pour le mammifère du poison de *Conus tessulatus*, considéré jusque là comme inoffensif;
- étude des enzymes de six espèces, de régimes alimentaires variés, et dont la sécrétion est, ou non, toxique pour le vertébré. La grande activité enzymatique observée n'est apparemment liée ni au régime alimentaire ni au degré de toxicité pour le vertébré;
- démonstration de la possibilité de détoxifier le venin du cône géographe par l'action du formol sans altérer son pouvoir immunogène d'où possibilité de préparer un sérum hyperimmun non dans un but thérapeutique mais pour disposer d'un moyen d'analyse des constituants du venin;
- mise en évidence dans le venin de deux constituants protéiques, inactivés par la pronase; l'un est un peptide de poids moléculaire compris entre 1500 et 2000.

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SciELO

LES OPHIDIENS DE MADAGASCAR

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RÉSUMÉ — Revue de la faune ophidienne de Madagascar et des principaux travaux qui lui ont été consacrés. Précisions sur certaines orthographes et attributions de noms d'auteurs: Bruguière; *Langaha* Lacepède, 1789; *Leioheterodon*; *Madagascarophis colubrinus*; *Mimophis mahfalensis*. Exposé des recherches récentes portant aussi bien sur la taxinomie classique ou sérologique que sur la morphologie des hémipénis, la faune parasitaire et les sécrétions venimeuses.

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1. INTRODUCTION

Une rapide présentation de la géographie physique de Madagascar est indispensable pour comprendre les milieux où vivent les animaux objets de nos préoccupations. Ces données peuvent se résumer en quelques chiffres:

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- 592.000 km², ce qui fait de Madagascar la plus vaste île de l'Océan Indien et la troisième du monde par son étendue;
- 1.580 km de long selon un axe à peu près Nord-Sud, qui s'étendent du 12^{ème} au 26^{ème} parallèles Sud, donc en presque totalité en zone tropicale puisque le tropique du Capricorne traverse l'île dans sa partie Sud, de part et d'autre du 45^{ème} méridien Est. L'importance de l'allongement dans le sens Nord Sud apparaît peut-être mieux lorsque l'on sait que la distance qui sépare les deux extrémités de l'île est la même que celle qui, dans l'hémisphère Nord, sépare la Norvège de la Méditerranée et, dans l'hémisphère Sud, au Brésil, Salvador de Curitiba.
- 2.500 m d'altitude, dans plusieurs massifs montagneux, ce qui, avec les plaines côtières et les séries de plateaux, crée nombre de compartiments assez bien isolés et aux climats variés.

La gamme des terrains géologiques est étendue: un ancien plateau granitique avec quelques régions volcaniques et un Ouest sédimentaire comprenant du triasique, du jurassique, du crétacé et du tertiaire.

Cette grande île qui, sur les cartes à grande échelle, semble accolée au flanc Sud-Est de l'Afrique, en est séparée par le canal de Mozambique. En son point le plus étroit celui-ci ne mesure que 392 km, mais, sur toute sa longueur, la profondeur du fossé dépasse 3.000 m. Les îles les plus proches sont les Comores à 300 km et les Mascareignes à 700 km.

Telle est la situation physique actuelle de Madagascar. Les progrès dans la connaissance de l'histoire du globe nous apprennent que les situations relatives des terres aujourd'hui émergées ont beaucoup évolué au cours des temps géologiques. Et les biogéographes qui avaient dû inventer des continents disparus et des ponts variés pour expliquer certaines affinités de flores ou de faunes ont maintenant d'autres supports pour asseoir leurs hypothèses. Qu'en est-il du Gondwana? Il n'est pas de mon propos d'en traiter aujourd'hui; de même je n'évoquerai pas les voyages océaniques supposés de la Grande Ile depuis la Pangée. Nous devons retenir que Madagascar qui, à l'échelle du globe, ne semble être qu'un appendice africain, est en fait séparée du continent par un fossé océanique qui, à en croire les géologues, existe depuis le triasique.

Une grande île, au relief varié, située en zone tropicale, proche de l'Afrique mais séparée d'elle depuis des millénaires, tels sont les principaux éléments physiques du décor où évolue, dans tous les sens du terme, la Vie malgache.

Qu'en est-il du milieu vivant?

Par leur étonnant degré d'endémisme, Flore et Faune malgaches offrent au naturaliste nombre d'énigmes phylogénétiques et biogéographiques. Et cependant d'innombrables espèces ont disparu, à la période historique, dans l'un et l'autre règne, sans laisser de traces depuis que la hache et le feu ont détruit la forêt qui les abritait. Madagascar avait eu la très grande chance, jusqu'à il y a quelques siècles, de ne pas être contaminée par l'espèce humaine. Mais celle-ci, arrivée tard, s'est, si l'on peut dire, rattrapée. L'homme n'a en effet atteint Madagascar qu'à la période historique, vers le IV^{ème} siècle de notre ère, cela lui a suffi

pour réduire à l'état de lambeaux le manteau forestier diversifié qui recouvrait, il y a quelques siècles encore, à peu près toute l'île. Paulian estimait, en 1955, qu'il ne restait qu'à peine 8 p 100 du couvert primitif. Depuis, la situation n'a cessé de se déteriorer. Combien de milliers d'espèces de plantes et d'animaux ont ainsi disparus à jamais qui étaient littéralement à portée de notre main? Les relictés que nous en observons ne font qu'augmenter nos regrets devant l'importance du désastre.

Pour nous en tenir aux Reptiles, et avant de passer aux Ophidiens, nous allons voir qu'ils présentent tout à la fois des rapports géographiques bien faits pour donner des migraines aux biogéographes et un extraordinaire endémisme.

La faune reptilienne ancienne est essentiellement marquée par la présence, au Mésozoïque, de Dinosaures, première énigme posée aux biogéographes. (*)

La faune reptilienne actuelle est caractérisée par

1. *Ses affinités africaines*: sont bien représentés, de part et d'autre du canal de Mozambique, les Chamaelionidés, les Scincidés et les Gekkonidés. La famille africaine des Cordylidés n'est présente à Madagascar qu'avec la sous-famille des Gerrhosaurinés.
2. *L'absence de grands groupes bien représentés en Afrique*: Amphisbaenidés, Varanidés, Agamidés, Lacertidés chez les Lézards, Elapidés et Vipéridés chez les Serpents.
3. *L'existence d'éléments inconnus en Afrique*: chez les Lézards, les Iguanidés, représentés par deux genres *Chalarodon* et *Oplurus* et chez les Serpents par des Boidés, sur lesquelles nous auront l'occasion de revenir longuement.
4. Un extraordinaire endémisme.

Nous traiterons en détails de l'endémisme des Ophidiens; pour les Lacertiliens dans une étude que nous avons faite en 1963, nous montrions que sur 32 genres de Lézards, 15 sont endémiques et que sur les 151 espèces 138 étaient endémiques soit un taux d'endémisme, au niveau spécifique, de plus de 91 pour 100. Les recherches plus récentes n'ont fait que confirmer ce haut degré d'endémisme de la faune reptilienne malgache.

Après une rapide présentation de l'histoire de l'acquisition de nos connaissances sur les ophidiens de Madagascar nous procéderons à une revue systématique d'ensemble avant d'aborder les domaines ayant fait l'objet de recherches récentes.

* Darlington 1957 : 535) semble bien oublier l'existence des Dinosaures lorsqu'il écrit: "Madagascar has an obviously old fauna, much differentiated, with many relicts and much radiation in some endemic groups On the other hand, the Madagascan fauna is evidently less old than the faunas of Australia and Tertiary South America. It may have begun to accumulate and evolve about the Oligocene."

Le dernier décrit, *Majungatholus atopus*, n.g. n.sp., l'a été en 1979, par Sues et Taquet.

2. HISTORIQUE.

A qui devons nous la connaissance de la faune des Ophidiens de Madagascar?

Dès la fin du XVIIIème siècle, les navigateurs et voyageurs naturalistes ramenèrent en Europe des représentants des faunes exotiques, témoins autant de leur curiosité que de leur audace et des dangers surmontés.

Le premier serpent malgache connu en Europe fût le Langaha que Bruguière signala en 1790. Près de cinquante ans plus tard, Schlegel publia la description de cinq espèces de serpents malgaches encore reconnues valables aujourd'hui. *L'Erpétologie générale* fit connaître en 1844 deux, puis en 1854 cinq autres espèces nouvelles. En 1858, Günther, dans sa revue sur la répartition géographique des reptiles n'attribue à la faune malgache que onze espèces (1a); mais relevant que la quasi-totalité de ces espèces n'a jamais été rencontrée en une autre région du monde il se demande si, comme l'avait déjà suggéré Schlegel, il n'y aurait pas là une raison suffisante pour considérer Madagascar comme une région géographique particulière: "small for the geographical area, rich for its animal and vegetative life, if the still hidden parts should prove to be as peculiar as that which we know." On ne connaissait encore que moins du quart de la faune ophidienne. C'est en effet entre 1880 et 1905 que furent décrites 28 espèces soit plus de la moitié de celles que nous reconnaissons. Le rythme des descriptions se ralentit ensuite, avec six espèces nouvelles entre 1913 et 1944. Les deux dernières décrites sont *Liopholidophis thieli* Domergue, 1972 et *Typhlops domerguei* Roux Estève, 1980. Les auteurs auxquels nous sommes redevables du plus grand nombre d'espèces nouvelles sont: Mocquard, 12; Günther, 9; Duméril et Bibron, 7; Boulenger et Boettger, chacun 6; Schlegel, 5. Sur les 17 genres endémiques, Mocquard et Günther en ont chacun créé quatre, Boulenger et Boettger chacun deux, les cinq autres étant dus à des auteurs divers.

Si la littérature consacrée aux serpents de Madagascar comprend de très nombreuses notes éparses dans des publications variées et traitant d'espèces nouvelles, de récoltes ou de discussions à leur sujet, par contre les travaux de synthèse, consacrés aux seuls Ophidiens malgaches, sont encore rares. La première monographie est due à Edmond Jourdran, en 1904, "les *Ophidiens de Madagascar*". Cet auteur est parmi les tous premiers à avoir largement utilisé les renseignements fournis par l'examen radiographique des spécimens. Les Serpents tiennent évidemment une place importante dans le *Synopsis* publié en 1909 par Mocquard sur les Reptiles écailleux et les Amphibiens de Madagascar. Boulenger en 1915 donna une liste des serpents de Madagascar et des îles de l'Océan Indien occidental. En 1922, Mme Phisalix, dans son monumental ouvrage sur "*Animaux venimeux et venins*" publia (2:280) un tableau des genres et espèces des Colubridae de Madagascar et des îles voisines et une définition des différents genres de Colubridés Opisthoglyphes, avec diagnose des espèces. Il s'agissait d'un véritable résumé de ce qui

(1a) L'une d'elle, *Herpetodryas bernieri*, est donnée, à tort, comme de l'Isle de France.

était alors connu de cette faune. Après avoir donné, en 1949, une révision du genre *Langaha*, J. Guibé publia, en 1958, un très important travail sur les Serpents de Madagascar. Depuis cette date le problème, dans son ensemble, n'a été abordé que par Ch. A. Domergue à l'occasion de la publication, en 1969, d'une Clé pour les serpents de Madagascar. Les auteurs qui, depuis 1909, date de la publication du *Synopsis*, ont le plus écrit sur cette faune sont, par ordre alphabétique, :

Fernand Angel, Charles A. Domergue, Jean Guibé, Robert Hoffstetter et Robert Mertens.

3. LA FAUNE OPHIDIENNE MALGACHE.

Sur les 10 ou 11 familles qui composent aujourd'hui le sous-ordre des Ophidiens ou Serpents (Guibé, 1970), quatre seulement sont connues de Madagascar et encore l'une d'elles, celle des Hydrophiidae n'y est-elle que très exceptionnellement représentée par les visites que peut faire sur ses côtes un serpent marin venimeux ubiquitaire, *Pelamis platurus* (Linné, 1765) (2). Decary (1950) assurait avoir, à deux reprises, vu un serpent marin dans la baie de Diégo Suarez mais sans avoir pu s'en emparer.

La faune des serpents terrestres de Madagascar appartient donc à trois familles, les Typhlopidae, les Boïdae et les Colubridae et comprend, dans l'état actuel des connaissances, 73 espèces réparties en 21 genres. Les 19 genres des deux familles Boïdae et Colubridae se décomposent en 9 genres monospécifiques, 5 genres bispécifiques et 5 genres avec plus de deux espèces, le plus riche étant *Pseudoxyrhopus* avec huit espèces.

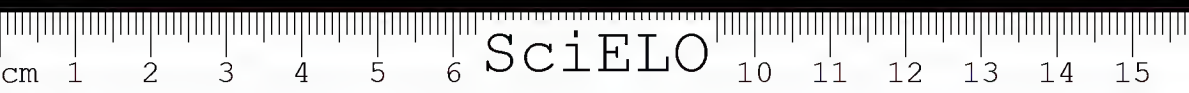
Si nous considérons l'endémisme, il est total pour les Boidae, deux genres et trois espèces, et presque total pour les Colubridae.

Dans cette famille, sur les 17 genres, 1 seul, *Geodipsas*, aurait des espèces sur l'Afrique continentale tandis que deux, *Liophidium* et *Lycodryas*, ont des représentants sur les îles Comores. Quatorze genres sont donc endémiques de la Grande Ile seule, comme le sont 60 des 61 espèces, *Lycodryas gaimardi* étant représentée par une sous-espèce à Mayotte.

Pour illustrer les nombreuses inconnues qui grèvent encore la connaissance de la faune malgache il n'est que de rappeler que 14 des 61 espèces de Colubridae ne sont connues que par les seuls spécimens types qui définissent aussi deux genres monospécifiques: *Compsophis* et *Heteroliodon*.

D'un point de vue pratique Domergue a donné en 1969 une "Clé simplifiée pour la détermination sur le terrain des serpents communs de Madagascar", particulièrement utile et qui doit son efficacité à la profonde connaissance qu'a l'auteur de cette faune malgache, basée, à l'époque, sur l'examen de plus de 700 spécimens recueillis sur le terrain.

(2) Boulenger (1915), Guibé (1958) admettaient la présence possible sur les côtes malgaches de *Disceiropsis schistosa* (Daudin, 1803), le premier sous le nom de *Enhydrina valakadyn* Boié, 1827 le second sous celui de *Enhydrina schistosa*. Mais selon McDowell (1972), cette espèce a une aire géographique beaucoup plus restreinte, du golfe Persique aux côtes du Vietnam et des Indes orientales à l'Australie.



Les trois familles sont d'importances très inégales mais chacune apporte son lot d'inconnues et de problèmes, du moins au spécialiste.

Nous présenterons rapidement les différents genres et espèces, rappelant les principaux travaux qui les concernent avant de donner un aperçu de quelques recherches thématiques récentes ayant porté sur la faune ophidienne de Madagascar.

4. LES TYPHLOPIDAE

Deux des trois genres actuellement reconnus (Hahn, 1980) dans la famille des Typhlopidae sont représentés à Madagascar, l'un et l'autre cosmopolites. Pour le non spécialiste ces ophidiens sont bien caractérisés par leur aspect vermiforme et leurs moeurs fouisseuses qui les font parfois confondre avec des vers de terre. Les créoles les nomment "serpent minute" nom qui, dans d'autres pays, évoque des reptiles autrement redoutables que ces animaux inoffensifs. Pour le systématique, l'anatomie de ces serpents aveugles, dont la mâchoire supérieure fixe est perpendiculaire au crâne, pose des problèmes passionnants. Leurs rapports avec les lézards semblent, sur bien des points, plus étroits que ceux des autres serpents.

Le genre ubiquiste *Typhlina* Wagler, 1830 n'a, à Madagascar, que son représentant cosmopolite *T. bramina* (Daudin, 1803). Des recherches récentes semblent établir que cette espèce est parthénogénétique. (McDowell, 1974).

Le genre *Typhlops* Oppel, 1811 possède à Madagascar huit espèces endémiques, encore très mal connues, trois d'entre elles, dont la dernière décrite (*T. domerguei* Roux-Estève, 1980) n'étant même représentée dans les collections que par le seul type (3).

Des deux sous-familles de Boidae, les plus primitifs des serpents vivants ainsi que l'atteste la présence de poumons complets et de vestiges de bassin et de membres postérieurs, ces derniers sous forme d'ergots ou de griffes sur les côtés du cloaque, seule est représentée à Madagascar celle des Boinae.

5. LES BOAS DE MADAGASCAR

Acrantophis et *Sauzinia*

Les problèmes phylogéniques et biogéographiques posés par les Boinés de Madagascar sont des plus complexes.

L'historique de la nomenclature des deux genres endémiques de Madagascar évoque bien les hésitations successives des auteurs qui s'intéressèrent à cette question. En 1844, Duméril et Bibron placèrent le nouveau boa qu'ils décrivaient dans le genre *Xiphosoma* Wagler, *X. mada-*

(3) Paulian (1961) signale la récolte d'un *Typhlops* sp sur le petit îlot corallien et sableux de Nosy Vorona, au Sud d'Androka.

gascariensis y rejoignait les deux espèces américaines *X. caninum* et *X. hortulanum* que ces auteurs admettaient. En 1849, Gray créa un genre nouveau, *Sanzinia*, pour y placer l'espèce malgache (4). En 1893, Boulenger plaça *Sanzinia* dans la synonymie de *Corallus* Daudin, 1803, ce qui fut accepté par Mocquard (1909) et Werner (1912). Stull (1935) réhabilite le genre *Sanzinia* qui n'a plus été discuté depuis.

C'est un nouveau genre *Pelophilus* que Duméril et Bibron créèrent, en 1844, pour le second Boïdé malgache qu'ils connaissaient: *P. madagascariensis*. Ce genre monospécifique fût accepté par Gray (1849). En 1860, Jan créa le genre *Acrantophis* pour l'espèce nouvelle *A. dumerili*. Boulenger (1893) plaça dans la synonymie de *Boa* Linné, 1758 à la fois *Pelophilus* D. et B. et *Acrantophis* Jan. Il signalait par la même occasion que *Pelophilus* était préoccupé (5) mais traitait *B. dumereli* et *B. madagascariensis* comme deux bonnes espèces. Mocquard (1909) reprend *Pelophilus* D. et B., à tort, et *Acrantophis* mais il n'est suivi ni par Boulenger (1915) ni par Werner (1921) qui maintiennent les deux espèces dans le genre *Boa*. En 1935, Stull réhabilita *Acrantophis* mais il fit de *dumerili* une sous-espèce de *Acrantophis madagascariensis*. C'est ce que suivait encore Mertens en 1955 et 1972 bien que dès 1949 Guibé eut démontré qu'il s'agissait de deux bonnes espèces, admises par Stimson (1969) lors de la dernière révision de la famille.

Le fait que les espèces malgaches furent, pendant longtemps, considérées comme appartenant aux genres néotropicaux *Boa* et *Corallus* montrait bien que ces serpents avaient plus d'affinités avec eux d'Amérique du Sud qu'avec les Pythones, représentants de la famille en Afrique et en Australie. Les Boïdés se séparent des Pythoninés par la perte de l'os supra-orbitaire et des dents prémaxillaires; les premiers sont vivipares, les seconds ovipares.

La création des genres *Sanzinia* par Gray en 1849 et *Acrantophis* par Jan en 1860, si elle marquait la singularité des espèces malgaches, ne résolvait évidemment pas le problème de leurs affinités et celui, sous-jacent, de l'origine du peuplement.

Romer (1956 : 573) créa une sous-famille des Sanziniinae:

"Similar to Boinae, but hypapophyses on all thoracic vertebrae" pour réunir aux deux genres malgaches les deux de l'île Ronde: *Bolyeria* Gray, 1842 et *Casarea* Gray, 1842. Mais Dowling (1959 : 45) démontra que cette sous-famille n'avait rien d'un groupe naturel et qu'elle était mal définie puisque Romer n'avait pas correctement utilisé les observations anatomiques de Hoffstetter (1946) et de Anthony et Guibé (1951). Ce que confirmait l'année suivante Hoffstetter (1960 : 137), après étude comparée des hypapophyses vertébrales des Boidae:

(4) non pour la raison donnée par Guibé (1949): "*Xyphosoma* Wagler étant tombé en synonymie avec *Boa*." car Gray (p. 96) reconnaissait le genre *Xiphosoma*. A noter que Gray ne donne aucune explication sur l'origine du nom du nouveau genre: "The Sanzin. *Sanzinia madagascariensis*. *Xiphosoma madagascariensis*." Y aurait-il un rapport avec le nom de Sganzin, mal orthographié? Duméril et Bibron écrivaient en effet à propos de cette espèce (1844 : 552): "Le Muséum en possède une belle suite d'individus de tous âges, que M. Sganzin avait commencé à former."

(5) Boulenger indique: "*Pelophilus* (non Dej.)." En fait le genre créé par Dejean en 1821 était *Pelophila*, ce n'était donc pas un synonyme au sens strict, mais deux autres *Pelophilus* antérieurs existent: *Pelophilus* Tschidí, 1838 et *Pelophilus* Eyton, 1841, celui de D. et B. ne pouvait donc être utilisé.

“Au contraire, *Acrantophis* et *Sanzinia* donnent des graphiques étonnamment comparables à celui de *Constrictor*. . . . Il en résulte que, sur cette base, il est impossible de séparer *Acrantophis* et *Sanzinia* des Boïnés. Les autres caractères squelettiques parlent aussi en faveur de leur rattachement à cette sous-famille.”

Dans un essai de subdivision de la sous-famille des Boinae, Underwood (1967) sépare la tribu des Bolyerini (de l'île Ronde) de celles des Erycini et Tropicophini, mais il se trouve toujours en présence d'un caput mortuum, la tribu des Boini, où voisinent un genre du Pacifique, *Candoia*, les 2 genres malgaches et les genres néotropicaux qui comprennent les grands Boas pour lesquelles la famille a été créé.

Les paléontologistes nous apporteront-ils, un jour la clef du problème? Un élément est pour le moment à retenir, Hoffstetter (1961) a rapporté au genre de Boïdé fossile *Madtsoia*, les vertèbres d'ophidiens recueillies dans le crétacé supérieur de la région N.W. de Madagascar par H. Perrier de la Bathie et par R. Lavocat; il a même, à cette occasion, créé l'espèce *M. madagascariensis*. Or *Madtsoia* est également connu du Paléocène de Patagonie (Hoffstetter, 1959). Aussi Mertens pouvait-il écrire (1972 : 92): “Eine andere Unterfamilie der Boiden, die fossilen *Madtsoiinae*, bildet ein Gegenstück zu den Boinae, da sie sowohl aus Südamerika wie aus Madagaskar bekannt sind.”

Pour l'instant, ainsi que l'écrivait récemment Branch (1981) :

“The phylogenetic relationships and zoogeographic history of boine snakes remains as intractable as ever.”

Et ce n'est pourtant pas faute de travaux anatomiques sur les Boïnés de Madagascar qui ont considérablement accru le domaine des connaissances.

Beddard (1906, 1908) après étude comparative des viscères de *Corallus madagascariensis* (= *Sanzinia madagascariensis*) et de *C. cooki* (= *C. enydris cooki* Gray 1842) écrivait :

“in view of the rather slender differences which often exist between genera among the Ophidia, it appears to me that the differences here recorded between *Corallus madagascariensis* and *C. cooki* are worthy of receiving value”.

En 1909, le même auteur établissait les différences anatomiques entre la constitution interne de *Boa (Pelophilus) madagascariensis* (= *Acrantophis madagascariensis*) et celle de *Boa occidentalis* (= *B. constrictor occidentalis* Philippi, 1873). En 1951, Brongersma étudia l'artère pulmonaire de *Acrantophis madagascariensis* et de *Sanzinia madagascariensis* et, en 1955, Anthony le squelette de la mâchoire et la morphologie dentaire, calculant différents indices osseux: maxillo-transverse, squamoso-sacré et dento-mandibulaire. Auffenberg (1958) s'intéressa à la musculature du tronc chez *Sanzinia* pour conclure :

“Myologically *Sanzina* (sic) is not as much like *Constrictor* as one would suppose. Deviations in muscular arrangement are suggestive of intermediacy between typical boïnes, such as *Constrictor*, and the Aniliidae, as represented by *Anilius*. The latter seems, in turn, intermediate between *Sanzina* (sic) and the Colubridae.”

Les travaux d'Hoffstetter (1959 : 382) furent consacrés à l'étude du dentaire tandis que ceux de Dowling (1959 : 3) montraient que les vertèbres de la région dorsale moyenne chez *Sanzinia* n'avaient pas d'hypapophyses. En 1963, Domergue étudia la morphologie des hémipénis des Boïdés malgaches et, la même année, Mme H. Genest-Villard le développement du crâne de *Sanzinia* montrant que, chez cette espèce, les os du crâne constituent un ensemble plus compact que chez les autres serpents accentuant la ressemblance du crâne des Boïdés avec celui des Sauriens. Underwood enfin (1976) montra que les relations entre os postorbitaux et les canaux vidiens rapprochaient les genre *Acrantophis* et *Sanzinia*, ce qui était selon lui un argument en faveur de l'hypothèse de Mertens (1972) de l'évolution des deux genres à partir d'un unique apport transocéanique (6).

Dés 1968, la Convention africaine d'Alger, sur la Nature et les Ressources naturelles, protégeait les deux représentants du genre *Acrantophis*, depuis les *Acrantophis* et le *Sanzinia* sont inscrits à l'annexe I de la Convention de Washington. Ces Boïdés, très spectaculaires et d'un maintien relativement facile en captivité, intéressent beaucoup les jardins zoologiques. En 1976, *A. madagascariensis* et *S. madagascariensis* étaient les seuls serpents signalés par le recensement des animaux rares établi par l'International Zoo Yearbook, le premier avec 33 spécimens en 15 collections vivantes, le second avec 42 en 18. Ces chiffres sont très au dessous de la réalité. Cette dispersion des animaux permet d'intéressantes observations sur le comportement et la reproduction (Mertens, 1955; Meier, 1980), nous y reviendrons plus en détails à propos de chaque genre. Nous verrons ultérieurement (7.4) ce que les recherches sérologiques ont pu nous apporter comme données nouvelles sur les rapports des Boïnés malgaches entre eux ainsi que sur leurs relations avec les autres espèces d'Ophidiens de Madagascar.

Pour le non spécialiste, à Madagascar, un Boïdé (7) se sépare des autres serpents terrestres par le plus grand nombre de rangs d'écailles dorsales, 40 à 80 pour un maximum de 33 observé chez le colubridé *Madagascariensis colubrinus*, ainsi que par une queue épaisse et courte. De plus les mâles présentent, de part et d'autre de la fente cloacale, des ergots mobiles, vestiges des membres postérieurs, qui interviennent dans les préliminaires d'accouplement.

5.1. *Sanzinia madagascariensis* (Duméril et Bibron, 1844) (8)

Ce serpent verdâtre, marqué de blanc, dont la tête plate élargie n'est pas sans rappeler celle des vipères, peut atteindre 2 m. Les jeunes sont brun noir et rouge orange. Branch et Erasmus (1976) signalent une variante jaune de *Sanzinia*, observée dans le Nord Ouest, mais sans modification de la lépidose: "it is doubtful whether yellow tree boas, despite having a restricted geographic range, deserve taxonomic recognition." La présence de fortes dépressions entre les plaques labiales supérieures

(6) L'on ne peut donc suivre W.R. Branch lorsqu'il écrit 1981 : 91) que la connaissance de l'anatomie de ces Boïdés est encore limitée; il semble ainsi ignorer nombre de travaux dont certains récents.

(7) De bonnes photographies en couleur des différents Boïdés de Madagascar sont publiées par Branch et Erasmus (1976) malheureusement des erreurs dans l'attribution des légendes compliqueront la tâche du non spécialiste.

(8) une bonne photographie de cette espèce in Blanc, 1972 : 614.

et inférieures est, chez cette espèce, tout à fait caractéristique. Elles correspondent à des fossettes sensoriales dont la localisation labiale est l'apanage des Boïdés et qui permettent à l'animal d'apprécier une différence de température de l'ordre de 0,2°C. Tous les genres de Boïdés n'en possèdent cependant pas et il est remarquable que la faune de Madagascar nous donne à observer un genre avec et un genre sans. (Maderson, 1970).

L'espèce est arboricole et l'on peut la rencontrer se reposant sur une branche d'arbre (9) mais il n'est pas rare de l'observer au sol.

Son régime alimentaire naturel, établi par les dissections, est basé de petits vertébrés, rongeurs et insectivores.

Nom vernaculaire: Manditra.

Le caryotype de *S. madagascariensis*, établi par Branch (1980), $2n = 34$, $NF = 50$, "is unique and not easily derivable from that of other pythons and boas." L'auteur souligne l'intérêt qu'aurait l'étude du caryotype des *Acrantophis*. A l'occasion d'études comparées chez les Vertébrés, Goswami et Rosenberg (1969) signalent la présence dans le foie de *Sanzinia madagascariensis* et de *Leioheterodon madagascariensis*, de parahydroxyphenylpyruvate hydrolase et de homogentisate oxygénase et l'absence de tyrosine alpha-cétoglutarate aminotransférase.

Au moins dans les débuts de sa captivité le *Sanzinia* peut être d'un tempérament agressif. Dowling et Spencook (1963) ont, semble-t-il les premiers, signalé des naissances en captivité, obtenues depuis par Foekema (1971, 1975), Groves et Mellendick (1973), Branch et Erasmus (1976) et bien d'autres. Progsha et Lehman (1970) ont, à cette occasion, signalés d'intéressantes malformations. Foekema (1975) a même obtenu en élevage une seconde génération, montrant que la maturité sexuelle était atteinte dès le 18^{ème} mois. La gestation est de 6 à 7 mois. Le nombre des jeunes, étudié sur 13 portées, varie de 1 à 16 avec une moyenne de 10,5, ce qui est inférieur à ce que l'on sait des autres boas arboricoles (Branch et Erasmus, 1976). La dimension moyenne du jeune est de 423 mm. Groves et Mellendick (1973) observent que les jeunes mâles se reconnaissent à leurs grands crochets anaux oranges alors que ceux des femelles sont plus petits et blancs. Ils signalent aussi qu'après une période d'alimentation assistée, alors que les jeunes se nourrissaient eux-mêmes de rongeurs nouveau-nés, l'un d'eux se singularisait en préférant grenouilles et salamandres.

5.2. *Acrantophis madagascariensis* (D. et B., 1844) et *A. dumerili* Jan, 1860. (10)

Ces deux boas, d'aspect extérieur très voisins, sont de teinte brune ou brun rouge, rehaussée de losanges noirs. Ils fréquentent les abords humides des cours d'eau et des mares. Duméril et Bibron (1844, 6 : 577) notaient déjà :

(9) L'attitude signalée par Blanc (1981) "ses anneaux repliés symétriquement de chaque côté de sa tête" n'a pas été observée par Branch et Erasmus (1976) qui écrivaient: "when basking in trees, both young and adults form a compact ball at the junction of a branch and never adopt the characteristic "draped" posture of *Corallus caninus* or *Chondropython viridis*."

(10) Une bonne photographie de *A. dumerili*, in Blanc, 1972 : 613.

“L’un d’eux avait dans l’estomac un canard dont toutes les parties étaient encore intactes, circonstance qui indique évidemment que le *Pelophilus madagascariensis* est un serpent aquatique.”

En fait, même s’il fréquente les points d’eau, l’*Acrantophis* n’est nullement aquatique et son régime alimentaire n’est pas à base de canards mais de petits vertébrés, rongeurs et insectivores comme nous l’ont montré de nombreuses autopsies.

Ces serpents sont de tempérament placide, ce qui explique leur utilisation éventuelle, encore qu’elle ne soit pas répandue, pour la lutte contre les rongeurs des cases par les habitants du Nord: *A. dumerili*, vu à Andranola par Kaudern (*in Anderson*, 1910).

Leur taille moyenne est de 150 à 180 cm. L’affirmation de Kaudern selon laquelle *A. madagascariensis* pourrait atteindre et dépasser 3 m de long a été confirmée par Decary qui signale un spécimen de 3m20.

Les *Acrantophis* furent un moment menacés par la chasse que leur faisaient les anciens militaires retour de France où ils avaient perdu une partie de leurs anciennes traditions qui protégeaient ces serpents. Les peaux étaient exploitées pour la maroquinerie. Ces aminaux sont aujourd’hui protégés.

A. madagascariensis est caractérisé par ses grandes plaques céphaliques, nettement différentes des petites et nombreuses plaques de *A. dumerili*. Leur nom vernaculaire est ‘Do’ ou ‘Ankoma’.

Alors que Guibé (1958) considérait que les aires de répartition des deux espèces étaient les mêmes, il semble que l’on puisse, selon nos observations, attribuer à *madagascariensis* une aire comprenant le Centre, le Nord Ouest et le Nord et à *dumerili* le Sud Ouest et le Sud ce qu’ont d’ailleurs signalé de leur côté Branch et Erasmus (1976). Pour ceux-ci “It is suggested that *A. dumerili* may represent a dwarf form.” “Nous verrons plus loin (7.2) que les différences sont plus profondes.

Très tolérants en captivité, les *Acrantophis* sont bien représentés dans les diverses collections vivantes. Duplaix-Hall (1974, 1975) est, semble-t-il, le premier à avoir signalé des naissances en captivité. Branch et Erasmus (1976) ont fait connaître d’intéressantes observations. La gestation est de 8 à 9 mois, les portées comprennent de 2 à 6 jeunes pour *A. madagascariensis*, 7 pour la seule observation concernant *A. dumerili*. Les jeunes sont exceptionnellement grands et peuvent atteindre chez *madagascariensis* 640 mm et 212 g soit 3 ou 4 fois le poids d’un jeune de *Boa constrictor* mais l’ensemble du poids de la portée est du même ordre dans les deux espèces. “It is suggested that. *A. madagascariensis* has evolved a reproductive strategy of few, but large young and that this may be correlated with the presence of few large predators on Madagascar.” La croissance est rapide.

6. COLUBRIDAE

La famille des Colubridae est de loin celle des Ophidiens la mieux représentée à Madagascar. Elle comprend 16 genres et 43 espèces, du moins dans l’état actuel de la connaissance et en faisant abstraction des



attributions fantaisistes erronées qui peuvent encore être publiée ici ou là (11).

Dans la présentation de la liste des Colubridae de Madagascar, donnée en annexe, nous n'avons pas tenu compte de la séparation, encore utilisée par Guibé (1958), entre Opisthoglyphes et Aglyphes, retenant la critique de J. Anthony (1955 : 51) :

“Les termes d'Aglyphe, d'Opisthoglyphe, de Protéroglyphe et de Soléroglyphe se rapportent à des états anatomiques d'origine parfois polyphylétique, et ne correspondent pas nécessairement à des catégories naturelles. Nous pensons, avec plusieurs auteurs modernes, que la conservation de ces coupures artificielles serait regrettable.”

Or les colubridae de Madagascar présentent une remarquable homogénéité : l'existence d'hypoapophyses vertébrales. Dès 1909, Mocquard (: 39) écrivait : “Il est remarquable que, chez tous les Colubridés malgaches aglyphes et opisthoglyphes, excepté, parmi ces derniers, les *Mimophis* et les *Eteirodipsas*, les vertèbres postérieures du tronc sont pourvues d'hypoapophyses.”

Depuis, l'*Eteirodipsas*, devenu *Madagascarophis*, ayant été reconnu comme ayant des hypoapophyses sur les vertèbres dorsales, l'homogénéité du lot est encore renforcée, en étant exclu le seul *Mimophis* qui se sépare d'ailleurs des autres par d'autres caractères. L'importance de l'observation de Mocquard était soulignée par Hoffstetter en 1946 qui ajoutait :

“La présence ou l'absence des hypoapophyses dans la région postérieure du tronc ne doit pas être négligée dans les discussions phylogénétiques concernant les Ophidiens. Ces hypoapophyses ayant une origine hypocentrale, il apparaît impossible (12) que des formes ayant perdu leurs hypocentra postérieurs aient pu donner des descendants qui les possèdent encore.”

L'ensemble des Colubridae de Madagascar se retrouve dans la sous-famille des Colubrinae, telle qu'elle est comprise par Romer (1956).

Nous allons d'abord voir le cas de ces *Mimophis* que plusieurs caractères séparent des autres Colubridés malgaches.

6.1. Les *Mimophis*.

Voyons d'abord le cas de ces Colubridae opisthoglyphes à pupille ronde rangés dans le genre *Mimophis* dont l'espèce unique est *M. mahfalensis* (Grandidier, 1867) (13).

(11) Elle peut parfois échapper à de très bons auteurs. Ainsi, par suite de quel enchaînement d'erreurs Mertens (1955 : 70) a-t-il pu écrire : “Die erste Natter, die aus Madagascar lebend in meinen Besitz kam, war ein *Sibynophis collaris*, eine Gattung, die ebenfalls in der Neuen Welt (allerdings auch in Südasien, aber nicht in Afrika) heimisch ist.”?

S. collaris (Gray, 1853) n'a jamais été récoltée à Madagascar, c'est une espèce du Sud-Est asiatique, du Nepal et de l'Himalaya.

(12) Nous ne discuterons pas ici de cette “impossibilité”, peut être beaucoup plus théorique que réelle.

(13) Grandidier avait utilisé l'orthographe phonétique “mahfalensis.” C'est cette graphie qu'emploient Boettger (1891), Mocquard (1895, 1909), Boulenger (1896, 1915), Anderson (1910), Mertens (1955). En 1904, Jourdran l'avait corrigé en “mahafalensis”, orthographe peut-être plus correcte, mais émendation injustifiée du point de vue du code de nomenclature et c'est à tort qu'elle est utilisée par Guibé (1958) et les auteurs qui l'ont suivie.



Le genre a été créé par Günther en 1868, pour une espèce qu'il croyait nouvelle, *M. madagascariensis*, mais qui, en fait, avait été décrite l'année précédente par Grandidier sous le nom de *Psammophis mahfalensis*. En 1891, Boettger cite les deux noms comme s'il s'agissait d'espèces différentes tandis que Mocquard, en 1895, établit la synonymie qui, adoptée en 1896 par Boulenger, n'a plus été remise en cause. Alors que pour Günther son nouveau genre était caractérisé, entre autres, par l'absence de loréale: "loréal none, replaced by the posterior frontal, which is bent downwards on the sides." Boulenger (1896) rectifia cette interprétation et distingua *Mimophis* de *Psammophis* par le fait que chez les premiers la préfrontale sépare la loréale de la préoculaire alors que chez les seconds loréale et préoculaire sont au contact.

L'originalité de cette espèce était bien soulignée par Mocquard (1895:103): "C'est probablement (en effet) le seul *Psammophidé* qui habite Madagascar..." Ces rapports étroits avec les formes africaines sont d'ailleurs à l'origine de diverses confusions avec les *Psammophis* africains. En 1877, Boettger donne comme de Madagascar *Psammophis sibilans*, *P. elegans*, *P. mahfalensis* et *Mimophis madagascariensis*, les deux premières espèces s'observant aussi en Afrique continentale. Mais 4 ans plus tard (1881:526) il exclut de la faune de Madagascar les deux espèces africaines et relève les erreurs d'identification ou d'attribution dont il a connaissance et dont la moindre n'est pas celle de Duméril et Bibron (1854, VII:895) qui les faisait donner *Psammophis sibilans* comme de Madagascar. Les rapports de *Mimophis* avec les *Psammophis* africains ne semblaient cependant pas évidents à Mertens (1955:72) qui écrivait:

"*Mimophis* wird im Schrifttum als die nächste Verwandte der äthiopisch-westasiatischen Gattung *Psammophis* bezeichnet; ich kann aber weder in der Körperform noch im Geben irgendeine Ähnlichkeit damit feststellen, sondern möchte die Verwandten von *Mimophis* unter neotropischen Nattern (*Dryophylax*?) suchen."

Par contre, en 1962, après étude de 50 spécimens mâles, Ch. A. Domergue pouvait écrire: "chez *Mimophis mahafalensis* (Boïginae), les pénis sont filiformes, inermes, absolument semblables à ceux que l'on connaît chez les Boïginae eurafricains... Les Boïginae malgaches possèdent des hypapophyses sur toute la longueur de la colonne vertébrale, *M. mahafalensis* fait exception à cette règle;... la denture de *M. mahafalensis* est, à peu de chose près, identique à celle du genre *Psammophis* (10 à 13 dents maxillaires, dont une ou deux agrandies au milieu de la série, précédées et suivies d'un espace libre, 2 crochets sillonnés postérieurs). Le type filiforme du pénis de *M. mahafalensis* lève les doutes qui pourraient subsister... aussi suis-je amené à considérer *M. mahafalensis* comme étant d'origine extra-malgache, susceptible d'être réintégré dans le genre africain et asiatique) *Psammophis* Boïé, 1827."

La coloration de cette espèce est assez polymorphe. Jourdran avait décrit et figuré une variété nouvelle *M. mahafalensis albiceps* dont l'existence n'a pas été confirmée. Par contre pour Domergue, l'auteur qui sans doute a manipulé le plus grand nombre d'ophidiens malgaches vivants, il existerait bien des variétés. En 1962 il écrivait (n. p. 102): "A noter que cette espèce unique se présente sous deux formes de coloration paraissant propres l'une à la région des Hauts-Plateaux, l'autre aux

régions Sud et Ouest.” et en 1969 (p. 15) : “il n'existe qu'une seule espèce du genre *Mimophis*, mais j'y ai reconnu au moins deux variétés de coloration, peut-être même deux sous-espèces : l'une propre aux régions Sud et Ouest, est de couleur uniforme chez la femelle ou avec une ligne vertébrale noire en zig-zag chez le mâle (*M. mahafalensis mahafalensis*), tandis que la forme des Hauts-Plateaux est pourvue de bandes noires parallèles (*M. mahafalensis lineatus*).” Il ajoutait en note “Ces deux formes et une troisième *intermedius*, sont en cours de description.” Ce qui n'a pas encore été fait.

Peu d'éléments ont été publiés sur la biologie de cette espèce, pourtant commune. Pour Mertens (1959:107), l'animal rappelle à s'y méprendre un rameau desséché et comme il reste longtemps complètement immobile, la tête tendue et inclinée, il échappe ainsi à l'attention de ses ennemis. L'observation de son ophiophagie, au moins occasionnelle, constatée par Jourdran sur une radiographie, n'a, en particulier, pas été confirmée. En captivité, Mertens (1955) lui a vu accepter petites grenouilles et lézards des murailles.

Selon Kaudern (*in* Anderson, 1910), dans la région de Ste Marie de Marovoay, cette espèce était appelée “Ombimati”, boeuf mort, par référence à la couleur de viande de boeuf.

M. mahafalensis peut atteindre 75 cm de long.

— x —

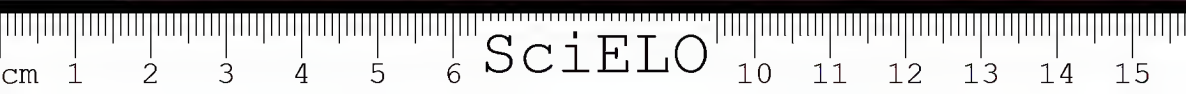
Mis à part le genre *Mimophis* et ses affinités africaines, il reste un lot assez homogène de 15 genres qui constituent le stock malgache des Colubridés, parmi ceux-ci les *Langaha*, les premiers décrits des serpents de Madagascar, alors qu'ils sont loin d'être particulièrement communs. Ils doivent sans doute à la forme particulière de leur appendice nasal d'avoir semblé digne de figurer parmi les trophées ramenés en Europe par Jean Guillaume Bruguière, docteur en médecine de Montpellier, qui accompagna Kerguelen dans son expédition aux îles australes. Il fit connaître à la communauté scientifique ce serpent remarquable sous son nom vernaculaire, *langaha*, dans le journal de Physique en 1784 (14).

— x —

6.2. Le genre *Langaha* Lacepède, 1789 (15)

Les représentants de ce genre sont tout à fait remarquables par un caractère unique, mis en évidence et bien étudié par J. Guibé (1948, 1949) que cet auteur résume ainsi (1970a:861-862) :

- (14) Alors qu'au XIX^{ème} siècle, le nom de Bruguière est le plus souvent correctement écrit, il fut transformé en Brugnère par Boulenger, à la suite sans doute d'une mauvaise lecture, lors de la publication de son catalogue (1896) et c'est ce nouveau nom qui fut utilisé par Mocquard et par Guibé. Au XIX^{ème}, le nom est écrit avec ou sans s finale, les deux formes se lisent dans Duméril et Bibron tandis que Schlegel (1837) et Jan (1863) écrivent le nom avec une s. Brogersma (1971) signala ces différentes orthographes.
- (15) L'attribution d'un nom d'auteur au genre *Langaha* a fait l'objet d'une discussion très argumentée par Brogersma (1972) qui démontre d'abord que Bruguière n'ayant, en 1789, donné qu'un nom vernaculaire, sans utilisation de la nomenclature binominale, ne peut être retenu comme l'auteur du genre. Il établit ensuite que le premier auteur à avoir usé de *Langaha* comme nom générique est Lacepède en 1789, mais comme par ailleurs il est d'avis d'exclure tous les noms de Lacepède, il propose que *Langaha* soit attribué à Bonnaterre, le second auteur à avoir utilisé le nom dans un sens générique (1790 : 71). Nous ne le suivons pas sur ce point et considérons Lacepède comme l'auteur de *Langaha*.



“Les Serpents malgaches du genre *Langaha* offrent un cas unique de dimorphisme sexuel, ils sont caractérisés par un prolongement écaillé rostral, flexible, dont la longueur égale à peu près celle de la tête; alors que chez le mâle ce prolongement est fin, de section triangulaire, chez la femelle il est large, foliacé, dentelé sur les bords qui sont repliés vers le bas en forme de gouttière renversée; de plus, chez *L. alluaudi*, la femelle possède une écaille susoculaire en forme de corne.” Selon Mertens (1959:154), qui ne précise pas l'origine de ses données, ces appendices joueraient un rôle dans la reconnaissance sexuelle, tandis que les animaux de ce genre possèderaient des yeux spécialement adaptés à la vie crépusculaire. Selon le même auteur l'existence des appendices contribuerait à accentuer la ressemblance avec des objets végétaux. En dehors de ces appendices remarquables, les recherches sur l'anatomie des *Langaha* n'ont, semble-t-il, pas donné lieu à de nombreuses publications. On peut signaler un dessin original du maxillaire et de la mandibule de *L. nasuta* donné par Mme Phisalix (1922, 2:352). Brongersma (1938) a vérifié l'existence d'hypapophyses sur les vertèbres précaudales d'un *L. cristagalli*.

Dans l'état actuel des connaissances, et après la révision de Guibé (1949b), ce genre de colubridés opisthoglyphes à pupille ronde, dont les représentants partagent avec les *Alluaudina* d'être les seuls de la faune malgache dont les écailles sont carénées, se compose de deux espèces:

— *Langaha nasuta* Shaw, 1970 (16)

(+ *L. cristagalli* D. et B., 1854 et *L. intermedia* Boulenger, 1888)

— *L. alluaudi* Mocquard, 1901.

La première espèce a deux loréales, la seconde une seule. Alors que les récoltes de *L. nasuta* proviennent de toutes les régions de l'île, celles de *L. alluaudi* ont pour origine la moitié sud. Les individus de l'une et l'autre espèce peuvent atteindre 1m. *L. nasuta* est bicolore, au dos brun rouge uniforme s'opposent la face ventrale et la lèvre supérieure jaune vif. (17). La femelle de cette espèce a une livrée plus terne, gris brun avec une série de taches rougeâtres, latérales. *L. alluaudi* est de couleur gris-cendré avec des bandes transversales foncées, plus ou moins nettes.

Le *Langaha* était déjà connu depuis plus de 50 ans lorsqu'en 1837 Schlegel décrivit quatre nouveaux serpents malgaches qui portent aujourd'hui les noms de *Madagascarophis colubrinus* (18), *Ithycyphus miniatus*, *Lycodryas gaimardi* et *Liophidium rhodogaster*.

(16) Dans son travail déjà cité, Brongersma (1972) donne les raisons pour lesquelles il propose a) de rejeter comme *nomina oblita*, les noms spécifiques qui n'ont plus été utilisés depuis 1833, 1. *L. madagascariensis* sous les formes *L. madagascar* Lacepède, 1790, *L. madagascar* Lacepède 1803 et *L. madagascariensis* Bonnaterre, 1790, 2. *Langaha* proposé en 1801 par Schneider dans le binome *Amphisbaena langaha*, b) mais par contre de retenir *Langaha nasuta* Shaw, proposé en 1802 sous la forme *Langaya nasuta*. Nous le suivons sur ce point. Une référence semble avoir échappé à Brongersma, dans ce travail par ailleurs si bien documenté, mais qui n'aurait rien changé à ses conclusions; il s'agit de l'article *Langaha* dû à Bory de Saint Vincent (in Dict. classique Hist. naturelle, 1826, 9 : 206) ou l'on trouve:

“Genre... établi par Lacepède sur un serpent découvert à Madagascar par Bruguière qui le fit connaître dans le journal de Physique en 1874.... On n'en connaît qu'une espèce.... C'est le *Langaha* Madagascariensis, Lacép.; *Amphisbaena* *Langaha*, Schneid.”

(17) La planche 71 de l'Atlas de l'Erpétologie générale 1854) présentait un *Langaha* crête de coq. Schmidt et Inger (1957) ont donné une bonne photographie d'une femelle de *Langaha intermedia* (= *L. nasuta*); cf aussi S. Dunton (Anim. Kingd. 1955, 58 : 142).

(18) C'est par erreur que Guibé (1958) et à sa suite Domergue (1969), Blanc (1971) écrivent *M. colubrina*. Le changement de nom (et de genre) du genre implique le changement d'orthographe du nom d'espèce ainsi que l'a d'ailleurs correctement écrit Mertens (1952, 1955).

6.3 *Madagascarophis colubrinus* (Schlegel, 1837)

Comme le remarquait Jourdran (1904 : 45), c'est une des espèces d'ophidiens de Madagascar les plus connues. Décrite par Schlegel dans le genre *Dipsas*, transférée dans un nouveau genre *Eteirodipsas* par Jan en 1863, elle est devenue l'espèce type et unique du nouveau genre *Madagascarophis* que créa pour elle Mertens en 1952, pour des raisons de nomenclature.

Ce colubridé opisthoglyphe à écailles lisses est d'une identification facile parce qu'il est le seul dont l'oeil, à pupille verticale, est séparé des labiales supérieures par des sous-oculaires (Guibé, 1958; Domergue, 1969). La tête, nettement distincte du cou, est triangulaire. L'animal est de coloration jaune verdâtre à gris noirâtre, avec des marbrures plus ou moins foncées. La variété du Sud présente de larges ocelles dorsales noires sur fond jaunâtre. De longueur moyenne 0,75 à 0,80 cm, il peut atteindre 1m. L'un des plus communs et des plus répandus des serpents malgaches, il traverse les routes et chemins aux premières heures de la nuit. Il est bien connu des habitants des Plateaux qui le nomme "Renivitsika" (19) ou mère des "fourmis" parce qu'il se trouve souvent dans les fourmilières et termitières. Selon une tradition rapportée par le Réverend Sibree et citée par Jourdran "les fourmis le nourrissent (dit on) jusqu'à ce qu'il soit gras puis le tuent pour le manger". Jourdran, par des dissections, a pu établir que le serpent, lui, ne mangeait pas de fourmis. En captivité, Mertens (1955) lui a fait accepter petites grenouilles, lézards et souris.

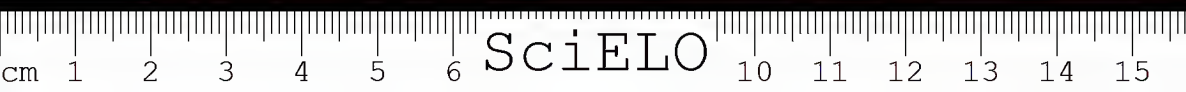
6.4 Les *Leioheterodon*

Les plus robustes des serpents de Madagascar, après les Boïdés, sont aussi parmi les moins rares; ils appartiennent au genre *Leioheterodon*. Aglyphes, à écailles lisses et pupille ronde, ils sont bien caractérisés par leur tête, peu distincte du tronc, qui porte une rostrale carénée, légèrement retroussée (20). Leur taille dépasse souvent le mètre et peut atteindre 1m 50.

Ce genre offre un bon exemple des difficultés que rencontre le systématien lorsqu'il s'efforce d'utiliser une nomenclature rigoureuse. La recherche de l'auteur du genre n'est, en effet, pas sans poser des problèmes qui ont déjà été étudiés par Myers (1949) mais la solution proposée alors, reposant sur des bases en parties fausses et surtout incomplètes, ne peut être retenue. Le nom de Léiohétérodon apparut pour la première fois sur une planche diffusée en 1844 avec le T. VI de l'Erpétologie générale qui abordait la description des Ophidiens. Cette planche porte le n° LXIX et la mention Léiohétérodon de Sganzin, elle présente une vue générale et trois bons dessins de la tête de l'animal. A la suite de difficultés diverses, la publication du tome VII de l'Erpétologie générale, avec la description de cette espèce, n'intervint que dix ans plus tard, en

(19) Ailleurs il se nomme "Lapato" (Sud et Sud-Ouest), "Mantertra" (Nord-Ouest).

(20) Mertens (1955 : 68; 1972 : 92), Schmidt et Inger (1957) rapprochent les espèces de ce genre malgache de formes nord-américaines et plus spécialement du Serpent à grouin d'Amérique du Nord (*Heterodon platyrhinos*) en raison justement de leur museau retroussé.



1854 (21). Duméril écrivit p. 776: "Heterodon de Madagascar. *H. madagascariensis nobis*. (Atlas pl. 69 sous le nom de Leiohétérodon de Sganzin." et p. 777: "Le nom de Leiohétérodon inscrit sur la planche 69 de notre Atlas ne peut être conservé, car il indique un caractère commun aux trois dernières espèces du genre *Heterodon* proprement dit et il n'y a pas de motifs réels pour subdiviser ce genre, comme nous l'avions cru d'abord". "On ne peut que regretter qu'avec le genre ait aussi disparu, sans explication, le nom de Sganzin, officier et naturaliste, dont les nombreuses récoltes sur la côte est de Madagascar et à sainte-Marie méritaient bien cet hommage. Le nom de Leiohétérodon apparaît encore p. 1553, dans la table alphabétique publiée à la fin de la deuxième partie du T. VII, ainsi que dans l'"Explication méthoque" publiée en 1854, en tête de l'Atlas qui réunit en un volume l'ensemble des planches précédemment publiées. Cette note précise, p. 15:

"planche LXIX. 1 *Heterodon* de Madagascar, représenté sous la dénomination provisoire de Leiohétérodon de Sganzin ... T. VII p. 776."

Ainsi que l'avait bien observé Myers, le nom de Leiohétérodon n'ayant, aucune des trois fois où il est utilisé par Duméril et Bibron, été écrit sous une forme latine, ce qu'atteste la présence des accents, n'a aucune valeur au sens du code de nomenclature. La première utilisation latine du nom de genre *Leioheterodon*, est semble-t-il (22), due à Jan (1863:227) à l'occasion de la création du genre *Anomalodon*, avec pour espèce type, par monotypie, *Heterodon madagascariensis* D. et B., 1854. Jan a ainsi créé, simultanément les deux noms de *Leioheterodon* et d'*Anomalodon*, synonymes objectifs. Boulenger, premier réviseur, a choisi le premier nom, plaçant le second en synonymie (23). Il a, de plus, procédé à une émendation, elle injustifiée, en proposant la forme *Lioheterodon*. Le nom de genre valable est, selon nous, *Leioheterodon* Jan, 1863 et non comme proposait Myers, *Lioheterodon* Boulenger 1893 (24).

L'espèce type en est *Heterodon madagascariensis* D. et B. 1854 par monotypie et non par la désignation secondaire de Myers, 1949. Guibé (1958:230), bien que donnant dans sa bibliographie la référence de Myers attribuait à Duméril et Bibron, avec la date de 1854, le genre *Lioheterodon* écrit avec l'orthographe proposée par Boulenger. Un auteur au moins, Conant (1938) a cependant, depuis Boulenger, utilisé l'orthographe correcte: *Leioheterodon*.

Pour Mertens (1972) ce genre n'est pas sans rappeler les genres du nouveau monde *Xenodon*, *Lystrophis* et *Heterodon*.

Alors que la séparation des trois espèces de *Leioheterodon* se fait, pour le spécialiste, sur la base de l'écaillure corporéale ou céphalique, les seuls caractères de coloration permettent à l'amateur une identification facile:

- (21) Ce décalage de dix ans entre les deux dates a échappé à Myers qui croyait à une erreur de Boulenger dans son catalogue.
- (22) Günther dans son catalogue (1858) ne mentionne pas *Leioheterodon*.
- (23) Myers signale d'ailleurs qu'*Anomalodon* Jan, 1853 est préoccupé par *Anomalodon* S. Bowdich, 1825, un poisson.
- (24) Le *Nomenclator zoologicus* créditait, en 1939. Boulenger (1893) du nom de genre *Lioheterodon* et ignorait le *Leioheterodon* de Jan (1863).

- noirâtre avec des taches jaunes au dessus, jaunâtre taché de noir au dessous, c'est *L. madagascariensis*;
- brun pâle uniforme: *L. modestus*;
- brun clair avec au dessus un réseau sombre formé par les lignes bordant les écailles: *L. geayi*.

Leioheterodon madagascariensis (D. et B., 1854)

Première décrite, cette espèce est aussi la plus grande des trois, elle atteint facilement 150 cm. Conant (1938) en a donné une bonne photographie (25) en même temps qu'il décrivait la ponte, en captivité, de treize oeufs, de dimensions moyennes 47,8 x 32 mm, pesant 28, 9 g. L'éclosion en eut lieu entre le 90^{ème} et le 96^{ème} jour. Les jeunes avaient une longueur moyenne de 336 mm et pesaient 18,68 g. Les enzymes hépatiques ont été étudiés par Gaswani et Rosenberg (1969).

L'animal est très actif et très vif, facilement agressif. Son nom vernaculaire: Manarana.

Leioheterodon modestus (Günther, 1863)

Décrivant *Heterodon modestus*, Günther semble avoir ignoré que Duméril et Bibron avaient déjà décrit l'animal, mais comme une variété de *L. madagascariensis* et sans la nommer:

"Une Variété est complément sans taches. Sa teinte générale est un fond brun jaunâtre. Elle provient comme le type de Madagascar et elle a été donnée par le même voyageur... L'échantillon unicolore qui se rapporte par tous ses caractères à l'espèce dans laquelle nous le rangeons est plus petit. Sa taille cependant montre que ce n'est pas un jeune individu."

Jourdran (1904) a proposé plusieurs bonnes représentations de cette espèce. Kaudern (*in* Anderson, 1910) signala son agressivité et le fait qu'irrité il était capable de gonfler son cou "like a cobra". Mertens (1955) l'a vu, en captivité, accepter de se nourrir de grenouilles.

6.5 Les *Pseudoxyrhopus*

Cette très belle espèce a son domaine localisé au Sud et au Sud-Ouest de l'île, alors que les deux autres se rencontrent dans tout Madagascar. Boettger (1913) en a donné une bonne illustration sous le nom de *Lioheterodon voeltzkowi* qu'il considérait comme une espèce nouvelle.

6.5 Les *Pseudoxyrhopus*

L'espèce type de ce genre remarquable a été crée par Jan en 1863 sous le nom d' *Homalocephalus heterurus*, nom que Günther (1881 : 359) transforma en *Pseudoxyrhopus*, celui de Jan étant préoccupé en Entomologie. Boulenger (1880 : 312) souligna les caractères particuliers de la denture de la machoire inférieure, rapprochant ce genre des Lycodonts. Dans le même travail il lui rapporte le *Xenodon punctatus* Peter, 1880:

(25) Par contre les couleurs de la planche originale de l'Erpétologie générale sont sans rapport avec les couleurs naturelles.



"Stated to be from Brazil, but its habitat will probably prove to be Madagascar". Cette espèce n'a semble-t-il plus été retrouvée depuis et les problèmes qu'elle pose n'ont pas été résolus. Les auteurs semblent cependant d'accord avec l'opinion émise par Mocquard (1909 : 45) :

"On peut affirmer que si *Xenodon punctatus* est un *Pseudoxyrhopus* il n'est pas originaire du Brésil, et que, s'il a réellement cette origine, il ne peut être rapporté au genre *Pseudoxyrhopus*."

Dans la révision de Guibé, ce genre *Pseudoxyrhopus* d'opisthoglyphes à pupille ronde est celui qui, avec ses huit espèces, semble le plus important ou du moins le mieux diversifié. En fait, selon Domergue (1969) trois espèces, *P. microps* Günther, 1881, *P. tritaeniatus* Mocquard, 1894, connues par le seul type, et *P. dubius* Mocquard, 1904 forment un groupe très homogène :

"la différenciation repose, . . . , sur des caractères peu convaincants . . . la validité de ces trois espèces peut être mise en doute tant leurs caractères d'écaillage sont voisins et pourraient bien ne représenter que trois variétés; aussi la distinction restera-t-elle délicate, pour ne pas dire impossible, et ces trois serpents pourront-ils, sans inconvénient, être considérés comme le groupe des *Pseudoxyrhopus* à vingt-cinq dorsales, avec trois sous-espèces ou variétés (ou peut-être seulement des aberrations individuelles d'une même espèce), toutes semblables par leur morphologie et leur coloration rouge à bandes longitudinales noires".

Boulenger avait déjà successivement mis en synonymie avec *P. microps*, en 1896, *P. trilineatus*, puis, en 1904, *P. dubius*, mais Angel (1935) avait cru pouvoir séparer les 3 espèces. Deux autres espèces, *P. ambreensis* Mocquard, 1894 et *P. occipitalis* Boulenger, 1896, ne sont connues que par les types. Restent 3 espèces *P. heterurus* (Jan, 1863), *P. quinquelineatus* (Günther, 1881) et *P. imerinae* Günther, 1890 mieux représentées dans les collections.

Boulenger (1915) faisait un *Pseudoxyrhopus* du *Rhabdotophis subcaudalis* Werner, 1909 que Guibé (1958) a placé dans la synonymie de *Pararhadinea melanogaster*.

6.6 Les *Ithycyphus*

Ce genre comprend deux espèces de Colubridae opisthoglyphes à pupille ronde, *Ithycyphus miniatus* et *I. goudoti* qui sont parmi les premiers décrits des serpents de Madagascar puisque l'un comme l'autre le furent par Schlegel en 1837, mais dans des genres différents, *Coluber* pour le premier et *Herpetodrias* pour le second. Le genre lui ne fût créé qu'en 1873, par Günther, pour une espèce, *Ithycyphus caudolineatus* que Boulenger plaça dans la synonymie d'*I. goudoti*. *I. miniatus* avait été décrit par Schlegel comme de l'Île de France (Maurice). Cette attribution erronée fût rectifiée par Duméril et Bibron en 1854, mais ceux-ci signalent des spécimens de Madagascar, Nossi Be et Mayotte. D'où mention par Boulenger, 1896, de la présence de l'espèce aux Comores, ce qui est encore repris, mais avec doute, par Blanc (1971). En fait l'espèce ne semble pas avoir été récoltée en dehors de Madagascar (et de Nossi Be).



L'espèce *Ithycyphus miniatus* n'est pas rare en forêt; elle est très caractéristique (26) avec sa longue queue rouge et ses moeurs arboricoles. Elle peut atteindre 1m 50 (Kaudern, *in* Anderson, 1910). Il semble établi que ce serpent puisse se laisser tomber d'un arbre sur les petits animaux dont il se nourrit. Bien connu des Malgaches qui le nomment *Pily* (saka-lave) ou *fandrefiala*, ce qui signifie "mesureur de la forêt", sans doute par référence a son habitude de se suspendre et de se déplacer de branche en branche, c'est, avec les boas et le *Menarana* (*Leioheterodon madagascariensis*), l'un des serpents que l'on rencontre le plus souvent dans les légendes. Accusé de nombreux pouvoirs, il serait en particulier capable de transpercer son ennemi, homme ou boeuf compris, en s'élançant ou en se laissant tomber queue la première (27). Ce serpent se nourrit entre autres de Caméléons. Nous en avons vu un spécimen qui, au moment de sa capture, venait d'engloutir un *Chamaeleo pardalis* mâle de plus de 35 cm. Kaudern (*in* Anderson, 1910) a, de son côté, trouvé un rat dans l'estomac d'un *I. miniatus*. Mertens (1955), qui en donne une bonne photographie, lui trouve quelques ressemblances de comportement avec le cubain *Dromicus angulifer*.

L'espèce *I. goudoti* se sépare de la précédente par son plus petit nombre de plaques ventrales.

6.7 *Dromicodryas*

Les deux espèces de colubridae aglyphes et à pupille ronde qui constituent ce genre furent, l'une et l'autre, décrite en 1854 par Duméril et Bibron comme des *Herpetodryas*. L'une d'elle avait même fait l'objet d'une planche (n° 66), diffusée en 1844, avec le nom provisoire d'Elaphre de Bernier. Boulenger (1896) créa pour elles le genre *Dromycodryas*, sans désigner d'espèce type. Domergue (1969) attira l'attention sur un caractère diagnostic: l'existence sur les ventrales "de chaque côté, d'un mince trait noir correspondant à une légère encoche et, peut-être à un soupçon de carène".

Les deux espèces, fort voisines, se caractérisent par leurs marques dorsales:

- trois bandes longitudinales noires chez *D. bernieri*,
- quatre chez *D. quadrilineatus*.

La répartition géographique exacte de ces deux espèces, qui ne sont pas rares, mérite d'être précisée car les localités de récoltes données par Guibé (1958) correspondraient à des aires en grandes parties communes. L'origine Ile de France donnée par Duméril et Bibron pour des spécimens de *D. bernieri* peut être considérée comme une erreur. Kaudern (1922) a décrit une sous-espèce *ramavali* de *D. bernieri* dont la valeur reste à préciser. Domergue (1969) a mis dans la synonymie de *D. bernieri* *Liopholidophis pseudolateralis* Guibé, 1956. Pour Kaudern (*in* Anderson,

(26) Jourdran (1904) en a donné une bonne planche (n.° 23).

(27) Il est intéressant de retrouver dans le folklore malgache une croyance qui pourrait bien appartenir au fond commun des craintes ancestrales de l'homme, les Grecs, en effet n'appelaient-ils pas *Acontias*, javelot, un serpent que l'on croyait s'élançant d'un trait sur les passants? Selon Kaudern (1922), sur la côte Est (Fandrarazana) il serait nommé "Iapara."

1910) les deux espèces se nourrissent essentiellement de grenouilles, dans le Nord Ouest *D. bernieri* étant nommée "rama vali" et *D. quadrilíneatus* "maro longa".

Jourdran (1904) a donné une bonne iconographie de ces deux espèces.

6.8. *Les Liopholidophis.*

Ce genre de colubridae aglyphes, à pupille ronde, endémique de Madagascar, est l'un des plus importants par le nombre de ses espèces. Il n'a été créé par Mocquard qu'en 1904 mais dès 1895 cet auteur écrivait, à propos de *Tropidonotus stumppi*:

"A l'exemple de M. Boulenger, je rapporte cette espèce au genre *Tropidonotus*, sans cependant être bien convaincu qu'elle ne doive pas constituer, avec d'autres espèces voisines, un genre particulier à Madagascar."

Ayant créé le genre *Liopholidophis* en particulier pour les espèces "...à vertèbres dorsales pourvues d'hypapophyses; hémipénis profondément bifurqués." Mocquard (1904) y plaçait une nouvelle espèce, *L. grandidieri* et les deux espèces *L. sexlineatus* et *L. dolichocercus*, dont Boulenger (1894) faisait des *Tropidonotus*, mais sans mentionner ni *T. stumppi* ni *T. lateralis*; il ne désignait pas d'espèce type. En 1909, Mocquard rappela le caractère particulier des hémipénis et ajouta que, dans ce genre, chez les mâles, "la queue est, en général, incomparablement plus longue que chez les femelles."

Ayant mis *T. stumppi* (28) dans la synonymie de *L. lateralis*, il reconnaissait alors dans le genre 4 espèces:

L. lateralis, *L. sexlineatus*, *L. dolichocercus* et *L. grandidieri*.

Depuis le travail de Domergue (1972) sur les *L. lateralis* s. l. la mise en synonymie (Domergue, 1969) de *L. pseudolateralis* avec *Dromycodryas bernieri*, ce genre comprend 6 espèces: *L. lateralis* (Duméril et Bibron, 1854), *L. stumppi* (Boettger, 1881), *L. sexlineatus* (Günther, 1882) (29), *L. grandidieri* Mocquard 1904, *L. pinguis* Parker, 1925 et *L. thieli* Domergue, 1972.

Chez les *Liopholidophis*, sauf exception, le ventre est jaunâtre ou blanchâtre, irrégulièrement taché (et non ponctué) de noir (Domergue, 1969).

Deux des six espèces, *L. pinguis*, du pays Sihanaka et *L. grandidieri*, du S. S. O, St Augustin, ne sont connues que par les types.

L. sexlineatus, de la région centrale et de l'Est, a une coloration très variable avec, typiquement, sur un fond gris olivâtre six bandes noires, mais celles-ci sont loin d'être toujours distinctes. Jourdran en a donné plusieurs représentations (pl 2, 15, 21, 25, 26). Il notait la longueur de la queue du mâle et signalait un spécimen de 1m20.

(28) *T. stumppi* était cependant encore reconnu comme espèce valide par Boulenger (1915) et par Parker (1925) mais ce dernier la plaçant dans le genre *Liopholidophis*.

(29) Guibe (1958 : 216) place *L. dolichocercus* (Peracca, 1892), espèce reconnue par Mocquard (1904, 1909), Boulenger (1896, 1915) et Parker (1925) dans la synonymie de *L. sexlineatus*.

Les recherches de Domergue (1972) ont débrouillé le groupe complexe des *L. lateralis* s.l. l'auteur conclut ainsi :

"Nous sommes en présence d'un groupe homogène dont les extrêmes sont *L. lateralis* et *L. thieli*; entre ces espèces parfaitement caractérisées se place *L. stumpffi* qui tout en étant reconnaissable d'entrée présente quelques individus de faciès apparenté tantôt à *L. lateralis*, tantôt à *L. thieli*; il semble que nous sommes en présence d'une espèce (*L. lateralis*) déjà suffisamment évoluée pour aboutir à l'espèce *thieli* et que les termes de passage, non seulement se sont conservés, mais encore semblent devoir eux-mêmes s'acheminer vers une espèce déterminée (*L. stumpffi*)."

L. lateralis est la couleuvre commune des jardins de Tananarive, ses moeurs sont semi-aquatiques et son régime alimentaire à base d'amphibiens, ce qu'avait déjà noté Jourdran. De vaste répartition dans l'île, elle ne semble manquer que dans le Sud-Ouest sédimentaire (Domergue). Selon Domergue, *L. thieli*, qui semble appartenir au domaine de l'est est connue dans la région de Perinet-Moramanga sous le nom de "Menamaso", oeil rouge, elle se nourrit également de batraciens. Ces deux espèces sont ovipares, avec des pontes de 6 à 13 oeufs elliptiques mesurant 24-27 mm x 12 mm.

Irritées, l'une comme l'autre, aplatissent dorsoventralement leur cou en attitude d'intimidation (30), l'élargissement latéral montre alors les marques blanches des écailles dorsales. *L. lateralis* peut se montrer très agressive et mordre énergiquement.

6.9. Les *Liophidium*.

Le genre *Liophidium* fut créé en 1896 par Boulenger pour une espèce malgache nouvelle, *L. trilineatum*, dont le dentaire est, en arrière, complètement séparé de l'articulaire. Il comprend aujourd'hui cinq espèces de colubridae aglyphes à pupille ronde, quatre de Madagascar et une des Comores. Guibé (1958 : 205, n) annonçait un travail "en cours de publication", fait avec le Dr Hoge, donnant "les raisons qui nous ont amené à inclure les genre *Idiophis* et *Parasibynophis* dans le genre *Liophidium*." Ce travail n'a malheureusement pas vu le jour. Le genre *Idiophis* avait été créé par Mocquard en 1901 pour l'espèce nouvelle *I. vaillanti*. Le genre *Parasibynophis* était dû à Leviton et Munstermann, en 1956, pour y placer les "*Polyodontophis*" de Madagascar. Après examen d'un *P. rhodogaster* (Schlegel, 1837) et d'un *P. torquatus* (Boulenger, 1888), comparaison des os maxillaires et craniens et des hémipénis, ils concluaient en effet à la nécessité de séparer ces deux espèces des autres représentants du genre, d'origine asiatique. Ils ajoutaient comme troisième espèce du nouveau genre *P. mayottensis* (Peters, 1873).

La séparation des deux genres est difficile sans une dissection permettant d'examiner les rapports du dentaire et de l'articulaire. Comme l'indiquait Mocquard dans la clef qu'il donnait en 1909, l'os dentaire est disjoint postérieurement de l'articulaire chez *Liophidium*, alors qu'il est

(30) Cette attitude, observée aussi par Mertens (1955) était pour lui un élément de rapprochement avec les genres néotropicaux *Liophis* et *Dromicus*.



articulé sur toute sa longueur avec l'articulaire chez *Liopholidophis*. La mise en synonymie par Boulenger (1915), avec doute, de *Liophidium gracile* Mocquard, 1908 avec *Tropidonotus stumpffi* (Bottger, 1881) puis par Guibé (1958) de ces deux espèces avec *Liopholidophis lateralis* (D. et B., 1854) souligne la difficulté du diagnostic sur les seuls caractères externes. Ce qui renforce l'intérêt des observations de Domergue (1969) :

"Les *Liophidium* ont le ventre soit franchement violace (...) soit rouge ou rougeâtre, ou rosâtre, avec des ponctuations régulièrement disposées en travers des ventrales, tandis que chez les *Liopholidophis*, sauf exceptions, le ventre est jaunâtre ou blanchâtre, irrégulièrement taché de noir."

A Madagascar s'observent quatre espèces *L. rhodogaster* (Schlegel, 1837) ; *L. torquatus* (Boulenger, 1888) ; *L. trilineatum* Boulenger, 1896 et *L. vaillanti* (Mocquard, 1901) qui ne sont pas rares et sont bien représentées en collection. Jourdran (1904) avait donné des représentations d'un jeune *L. vaillanti* (Pl 6) et d'un *L. torquatus* (Pl 6). La présence de *L. vaillanti* à la Réunion, signalée par Guibé (1958), reprise par Blanc (1971), demande à être confirmée car cette localisation ne repose, pour le moment, que sur un spécimen du Muséum de Paris dont les conditions d'entrée en collections laissent subsister quelques doutes quant à son origine réelle.

Avec ce genre nous rencontrons le premier des deux genres d'ophidiens malgaches ayant des représentants au Comores. *L. mayottensis* (Peters, 1837) a été décrit comme *Ablades (Enicognathus) rhodogaster* var. *mayottensis* ce qui soulignait bien ses affinités avec l'espèce de la Grande Ile, si bien caractérisée par la coloration rouge-violacée de son abdomen, encore nette sur les sujets conservés depuis longtemps en alcool. Cette forme, endémique de Mayotte, fût placée dans le genre *Polyodontophis* par Boulenger (1896) qui lui reconnut le statut d'espèce. Leviton et Munsterman (1856) la placèrent dans le genre *Parasibynophis* avant que Guibé (1958) ne la transfère dans le genre *Liophidium*.

6.10. Les *Lycodryas*.

Les *Lycodryas* sont des colubridae opisthoglyphes à pupille verticale de Madagascar et des Comores. En 1958, Guibé mit en synonymie le genre *Stenophis*, créé par Boulenger en 1896, pour des serpents de Madagascar et des Comores avec le genre *Lycodryas* créé près de vingt ans plus tôt par Günther (1879) pour une espèce des Comores :

"La séparation des genres *Lycodryas* Günther et *Stenophis* Boulenger ne repose en fait sur aucun caractère valable."

Alors que dans le genre *Liophidium* il s'agissait d'un genre malgache ayant une forme aux Comores, il semble bien qu'ici que nous ayons un genre appartenant réellement aussi bien aux Comores qu'à Madagascar. Les espèces malgaches sont théoriquement au nombre de 6 avec une sous espèce mais deux espèces : *L. variabilis* (Boulenger, 1896) et *L. inornatus* (Boulenger, 1896) ne sont connues que par les types. On peut s'interroger sur leur validité lorsque l'on garde en mémoire l'observation de Guibé (1958) : "Les espèces du genre sont remarquables par la grande variabilité de leur écaillage."



L. gaimardi (Schlegel, 1837) fût l'une des premières décrites des espèces de Madagascar. Pour Jourdran (1904) c'est: "La plus belle forme, peut-être de tous les serpents de Madagascar, la plus jolie comme coloration"; cet auteur en donne deux représentations (Pl 6 et 18).

Cette espèce est en effet bien caractérisée par la série de bandes transversales foncées.

Guibé (1958) a ramené au rang de sous-espèce de *L. gaimardi* *Stenophis granuliceps* Boettger, 1896 dont Mocquard (1909) et Boulenger (1915) admettaient la validité. Par ailleurs le même auteur suit Boulenger et place *Dipsas* (*Heterurus*) *gaimardi* var. *comorensis* Peters, 1873, connu par un juvénile de Mayotte, dans la synonymie de la forme nominale. *L. gaimardi gaimardi* serait ainsi la seule espèce à avoir des représentants à la fois à Madagascar et aux Comores.

Les *Lycodryas* des Comores comprennent deux espèces: *L. maculatus* (Günther, 1858) et *L. sanctijohannis* (Günther, 1879). Jusqu'en 1970, *L. maculatus* n'était connu que par le type, un mâle d'origine inconnue. Décrivant deux femelles de cette espèce en 1970, Domergue pouvait en préciser la terra typica puisque l'une provenait de Grande Comore et l'autre de Mohéli.

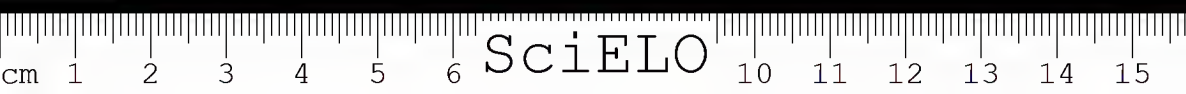
L. sanctijohannis Günther, 1879 avait d'abord été décrit d'Anjouan. Boettger (1913) proposa la création d'une variété *mayottensis* pour un spécimen rapporté de Mayotte par Voeltzkow. Les collections du Muséum de Paris possèdent des spécimens d'Anjouan, de Mayotte et de la Grande Comore. Boettger (1913) avait déjà signalé la présence de l'espèce dans cette dernière île.

6.11 Les *Geodipsas*

Avec les *Geodipsas*, genre de colubridae opisthoglyphes et à pupille ronde, nous rencontrons le seul taxon de cette famille ayant à la fois des espèces en Afrique et à Madagascar, en nombre égal d'ailleurs, 3 de chaque côté. Celles d'Afrique sont observées au Cameroun, au Zaïre et en Afrique orientale.

Le genre *Geodipsas* a été créé en 1896 par Boulenger pour deux espèces malgaches décrites dans le genre *Tachymenis*: *T. infralineata* Günther, 1882 et *T. boulengeri* Peracca, 1892, sans désignation d'espèce type. En 1936, Angel ajouta une troisième espèce *G. heimi*. Mais *G. boulengeri* et *G. heimi* ne sont connus que par les seuls types, si l'on y ajoute qu'Angel lui-même considérait son espèce comme très proche de *boulengeri* et que l'une et l'autre espèce proviennent de la même région de Madagascar, la vallée de l'Onive (*G. boulengeri*) et celle du Sahandrato (*G. heimi*), appartenant donc toutes deux au domaine de la région Sud Est, on ne peut que se poser des questions sur la validité d'au moins l'une de ces deux espèces.

L'espèce *G. infralineata* est beaucoup mieux représentée dans les collections. Décrite de l'est du pays Betsileo elle a été récoltée dans la région Est et sur les plateaux. Un couple, du à Paulian, vient du Tsaratanana (2.000m), un spécimen de la gaine d'un Ravenala de Périnet.



6.12 Cinq genres à espèces "rares"

Pour être complète, cette présentation de la faune ophidienne malgache doit se poursuivre par l'énumération d'un certain nombre de genres et d'espèces connus par de très rares spécimens et souvent par les seuls types, ce qui à la fois souligne l'extraordinaire richesse de cette faune et la grande nécessité d'organiser des prospections systématiques avant que l'évolution inexorable qu'entraîne la destruction des biotopes n'ait fait disparaître à jamais les témoins d'une vie reptilienne si richement diversifiée.

Le genre *Alluaudina* comprend deux espèces de colubridae opisthographes à pupille ronde, l'une de l'extrême nord (*A. bellyi* Mocquard, 1894), l'autre du nord-ouest (*A. mocquardi* Angel, 1939) ; le type de cette dernière espèce a été découvert par Decary, engourdi et roulé sur une console stalagmitique dans une grotte totalement obscure de la Mananjeba. Les représentants de ce genre sont les seuls ophidiens à Madagascar, avec les *Langaha*, à avoir des écailles carénées.

Deux autres genres de colubridae, aglyphes à pupille ronde, ont en commun de n'être connus que par un seul spécimen juvénile : *Compsophis albiventris* Mocquard, 1894 de la montagne d'Ambre et *Heteroliodon torquatus* Boettger, 1913 de la région de Tuléar. Schmidt et Inger (1957) considèrent cette dernière espèce comme une forme fouisseuse, en raison de "son nez en pelle". C'est peut être aller un peu vite en besogne. Des données complémentaires sont nécessaires.

Pour les deux derniers genres cités, qui sont encore des colubridae aglyphes à pupille ronde, eux aussi monospécifiques, dont les types proviennent pour l'un et l'autre de Nossi Be, la situation est à peine meilleure : *Micropisthodon ochraceus* Mocquard, 1894 dont Guibé (1958) ne signale l'existence que de deux exemplaires alors que pour Domergue (1969) il y en aurait 4 de connus, et *Pararhadinea melanogaster* Boettger, 1890, connu par deux spécimens dont l'un est le type de *Rhabdophis subcaudalis* Werner, 1909 que Boulenger (1915) plaçait dans le genre *Pseudoxyrhopus* et dont Guibé (1958) a fait un synonyme de *P. melanogaster*.

7. RECHERCHES RÉCENTES

La prospection de la faune ophidienne malgache au cours des vingt dernières années s'est accompagnée d'un certain nombre de recherches qui, dépassant le simple domaine faunistique dont l'importance ne doit d'ailleurs en aucun cas être sous-estimé, avaient pour but soit de fournir des éléments susceptibles d'apporter une aide à la systématique comme l'étude des hémipénis et celle de la sérologie soit de préciser la place des serpents dans les écosystèmes comme l'étude des poisons et celle des parasites.

Nous passerons rapidement en revue ces quatre domaines.

7.1 Recherches sur les Hémipénis

Dès 1893, E. D. Cope attribuait une importance particulière à la configuration de l'hémipénis pour venir à bout des incertitudes de la systématique des Ophidiens. Cette idée ne fût pas facilement admise et il fallut attendre 1928 pour voir paraître des travaux importants sur ce sujet. Ce fût d'une part Z. R. Dunn qui classa les Colubridés américains par leur caractères penniens et d'autre part J. Vellard qui fit connaître les résultats de ses travaux au Brésil et singulièrement à l'Institut Butantan. Ce même auteur, presque vingt ans plus tard, en 1946, donna la synthèse de ses observations, insistant sur l'intérêt de l'étude de l'évolution de l'hémipénis pour établir la phylogénie des Serpents (31). L'idée avait fait son chemin et divers auteurs utilisent aujourd'hui ce caractère anatomique. En Afrique, une application systématique en fut faite par Bogert (1940) qui examina l'hémipénis d'une espèce malgache, *Liophidium torquatus*. En 1956, ce fut l'examen par Leviton et Munsterman des hémipénis de *Liophidium torquatus* et de *L. rhodogaster*. Depuis 1962 une attention particulière est portée à l'étude de ce caractère par Ch. A. Domergue, mais dès 1904, F. Mocquard utilisait le caractère bifurqué des hémipénis pour séparer le nouveau genre *Liopholidophis* qu'il créait, de l'ancien genre *Tropidonotus*:

"..... il importe de le remarquer, on ne les (les hémipénis bifurqués) rencontre pas en même temps que les hémipénis simples chez les espèces d'un même genre homogène".

En 1962, Domergue décrivait l'hémipénis de *Mimophis mahfalensis* dont nous avons déjà vu l'intérêt biogéographie et phylogénique. Dans le même travail il faisait connaître les grandes lignes de la structure de celui de *Liopholidophis lateralis* "pénis franchement divisé, à branches très aplaties, de forme remarquable parmi ceux des espèces que j'ai observées jusqu'ici". Un an plus tard, en 1963, il écrivait:

"A l'exception du genre *Mimophis*, les pénis des 17 espèces examinées présentent la division du sillon et deux apex; chez 16 espèces, les apex sont portés par des branches distinctes plus ou moins développées, tandis que chez la 17ème, *Madagascarophis*, les branches sont coalescentes". En 1972 il publia des dessins des hémipénis de *Liopholidophis lateralis* et d'une nouvelle espèce *L. thieli*. Ch. A. Domergue a réuni une masse d'observations considérable sur la faune ophidienne de Madagascar et en particulier sur la morphologie des hémipénis de nombre d'espèces, il est souhaiter qu'il ne fera pas trop attendre la publication de ces éléments indispensables pour la connaissance des serpents de la Grande Ile, ainsi que la publication de sa Faune des Ophidiens de Madagascar annoncée depuis 1962. Le dernier travail sur des hémipénis de serpents malgaches est sans doute celui de W. Branch (1981) qui étudia ceux des Boïdés *Acrantophis* et *Sanzinia* sans d'ailleurs y trouver la solution sur l'origine des Boïdés de Madagascar.

(31) On ne voit pourquoi Dowling écrivait en 1967:

"However, only Dunn (1928) and Bogert (1940) have attempted to use it (the hemipenis as a taxonomic character) as a major character in colubrid classification in recent times..." ignorant ainsi l'importante contribution de Vellard alors que le même auteur, en collaboration avec Savage, avait écrit en 1960:

"Vellard (....) is the only other student to deal with hemipenial features as they relate to problems of major classification."

7.2 Sérologie

En 1969, avec Ch. A. Domergue, Dodin et Pinon nous avons utilisé la technique de la double diffusion en gélose pour l'étude des constituants sériques d'un certain nombre de serpents malgaches. Chez les Boïdés, le sérum anti-*Sanzinia* qui donnait sept lignes de précipitation en présence du sérum homologue, n'en donnait plus que cinq avec les sérums d'*Acrantophis*, sans qu'il soit possible de mettre en évidence une différence selon l'espèce d'*Acrantophis* en cause. Ce même sérum ne donnait qu'une seule ligne de précipitation en présence des sérums des neuf espèces de Colubridés testées. Pour les Colubridés nous avons préparé trois anti-sérums, un avec chacune des espèces de *Leioheterodon*. Nous avons retrouvé sept systèmes précipitants chaque fois que l'antisérum était mis en présence du sérum homologue, par contre, lorsque l'antisérum était mis en présence du sérum de l'une des deux autres espèces il ne donnait plus que six bandes de précipitation apportant ainsi une confirmation sérologique à la valeur des trois espèces. En prenant comme système de référence les protéines de *Leioheterodon modestus*, les genres de Colubridés de Madagascar se classent, du point de vue sérologique, en raison de leur affinité décroissante pour *Leioheterodon*, de la manière suivante:

- a) *Langaha*, *Mimophis* et *Dromycodryas*, cinq systèmes de précipitation,
- b) *Micropisthodon* et *Lycodryas*, quatre systèmes de précipitation,
- c) *Liopholidophis* et *Pseudoxyrhopus*, trois systèmes de précipitation,
- d) *Madagascarophis*, deux systèmes de précipitation,
- e) *Ithycyphus*, un système de précipitation.

Il est tout à fait remarquable que du point de vue sérologique le genre *Ithycyphus* n'a pas plus d'affinité avec *Leioheterodon* que n'en ont les Boïdés. On relèvera également que parmi les trois genres ayant le maximum d'affinités sérologiques avec *Leioheterodon*, genre de serpents aglyphes, se trouvent un genre d'aglyphes (*Dromycodryas*) et deux genres d'opisthoglyphes (*Langaha* et *Mimophis*).

L'année suivante nous avons repris ces recherches en utilisant l'immunoélectrophorèse et en introduisant un sérum anti *Madagascarophis colubrinus*. Il est apparu que la technique de double précipitation en gélose permettait une meilleure sélectivité des résultats que celle l'immunoélectrophorèse.

Ces techniques trop peu utilisées, encore qu'une publication toute récente de Schwaner et Dessauer (1981) étudie les relations des Boas papous par immunodiffusion, peuvent être d'un grand secours pour l'étude des espèces dont les captures d'individus sont rares, empêchant ainsi toute étude biométrique. Leur intérêt doit rester présent à l'esprit de tout récolteur. La grande diffusion des moyens de congélation rend moins improbable l'éventualité de pouvoir conserver dans de bonnes conditions, au fins de recherches ultérieures, le sérum d'un spécimen qu'il ne serait pas possible de conserver vivant.

7.3 Parasitologie des Ophidiens de Madagascar

Depuis un peu plus de 20 ans, la faune parasitaire des Ophidiens de Madagascar a fait l'objet d'une importance série de travaux, en particulier sous la direction et l'impulsion d'Alain Chabaud et de ses élèves. La liste des résultats acquis est donnée en annexe (9.4).

La faune parasitaire des Boïdés malgaches présente un intérêt particulier car l'on sait les secours que l'on attend parfois de la parasitologie pour éclairer tel problème de systématique ou de biogéographie. Au stade actuel des connaissances trop d'inconnues demeurent en ce qui concerne la faune parasitaire des Boïdés en général pour que soit venu le temps des comparaisons utiles. Les observations faites à Madagascar n'en sont pas moins dignes d'intérêt. C'est ainsi que l'on note chez les Boïdés la présence d'un pentastome porocéphale qui est loin d'être rare dans les poumons de ces Ophidiens.

Sur du matériel récolté en 1898, par A. Mocquérys, les formes adultes "chez un serpent dont l'espèce et le genre n'ont pas été mentionnés" et les formes nymphales dans le foie et le poumon d'un "hérisson", Gilioli créa en 1922 l'espèce *Armillifer brumpti* (32). En 1954, après la découverte de formes nymphales chez un Lémurien, Chabaud et Choquet conclurent qu'il ne pouvait s'agir d'une espèce du genre *Armillifer* et créèrent pour elle le nouveau genre *Gigliolella*. Les rapports entre ce genre et les autres représentants de l'ordre des Porocephalida n'ont, semble-t-il, pas été discutés depuis. Peut-être y a-t-il là une voie de recherche intéressante. Les larves et nymphes de ce pentastome ne sont pas rares chez les insectivores malgaches, proies naturelles des *Acrantophis* et *Sanzinia*. Nous les avons rencontrés chez *Tenrec ecaudatus*, *Hemicentetes semispinosus* et *Oryzoryctes talpoides*. L'infestation au laboratoire des souris blanches se fait sans difficulté (Brygoo, 1963). *Acrantophis dumerili* est également l'hôte d'un pentastome céphalobaenidé, *Mahafaliella tetrapoda* Gretillat, Brygoo et Domegue, 1962; mais ce parasite beaucoup plus rare, n'a sans doute pas le même intérêt que le *Gigliolella* pour des études comparatives.

Parmi les parasites d'ophidiens malgaches nous ne citerons encore que l'*Hepatozoon domerguei* du *Leioheterodon modestus* parce que l'étude expérimentale de cette espèce a permis à Irène Landau de découvrir des mécanismes fondamentaux assurant la perennité de l'infection chez les sporozoaires coccidiomorphes et en particulier l'existence d'une endogénèse et d'un double cycle de transmission.

Salmonelles.

Bien qu'il ne s'agisse pas de parasites au sens strict, on ne peut traiter des hôtes des serpents sans évoquer des bactéries qui peuvent avoir un rôle en pathologie humaine, les salmonelles. A Madagascar, comme ailleurs, les Serpents sont les hôtes naturels et par là même des disséminateurs dont le rôle ne peut être négligé de ces agents pathogènes.

(32) Gilioli notait justement l'absence de hérisson à Madagascar mais il se trompait quand il croyait pouvoir affirmer que l'hôte était un Tenrec. L'insectivore malgache qui, par son apparence extérieure, ressemble le plus à un hérisson européen est le *Setifer setosus*, c'est donc probablement lui le "hérisson" de Mocquérys.

Voici près de 20 ans déjà, P. Le Noc publiait une première note où il regroupait les résultats de l'isolement des salmonelles chez les Serpents. Depuis les recherches en ce domaine se sont poursuivies à l'Institut Pasteur Madagascar et en 1978, Lhuillier, Zeller et Leminor pouvaient en donner un bilan particulièrement évocateur puisque le tableau récapitulatif comprend 33 sérotypes différents, isolés de serpents, dont de nombreux découverts pour la première fois à Madagascar.

7.4. Serpents malgaches et Poisons.

Il peut paraître curieux de traiter des poisons de serpents malgaches alors que l'une des caractéristiques de la faune de Madagascar, célébrée par tous les voyageurs et explorateurs, était justement l'absence d'animaux venimeux. Comme toujours la nature, infiniment complexe, ne nous permet pas d'établir des divisions aussi tranchées.

Sept des 16 genres de Colubridae de Madagascar sont constitués de serpents opisthoglyphes, avec parmi eux certaines des espèces les plus répandues, aussi l'éventualité d'accidents d'envenimation ne peut-elle être exclue a priori. De fait, deux cas de morsure avec envenimation, tous deux du à *Madagascarophis colubrinus*, ont été signalés. Le premier par Mertens (1955) qui écrit simplement, à propos de ce serpent :

"deren Biss nicht eben angenehm ist, wie wir erfahren mussten, als eine Laborantin beim Auspacken eines solchen Tieres gebissen wurde." Le second par Domergue (1964) qui donna une observation beaucoup plus complète. Une morsure à la première phalange de l'index s'accompagna des symptômes suivants :

"Apparition quasi-immédiate d'une tache hémorragique aux points de morsure, évoluant en escarre; développement rapide d'un oedème intense, mais qui restera localisé à la main et à l'avant-bras; absence de suffusions sanguines et de traces hémorragiques éloignées; absence de troubles généraux." L'oedème de la main persista huit jours, celui du doigt trois semaines avec nécrose de la région mordue.

Mais les Opisthoglyphes ne sont pas les seuls à élaborer des substances venimeuses. Domergue et Richaud (1971) ont ainsi pu démontrer l'existence d'une activité hémolytique des sécrétions des glandes de Duvernoy chez *Leioheterodon*. Ayant noté, à la suite d'une morsure accidentelle par un *L. geayi*, un retard de coagulation ces auteurs ont expérimenté avec les glandes de *L. geayi* et de *L. modestus*. L'extrait de glande injecté à la souris par voie intrapéritonéale la tue d'hémorragie en 20 minutes, cet extrait n'est pas actif sur le lézard *Oplurus*. In vitro les globules rouges de souris, de lapin et de poule sont hémolysés, plusieurs enzymes sont en jeu. Mais cette propriété de la sécrétion de la glande de Duvernoy n'est pas générale, ainsi que l'a montré l'absence de réaction de la souris après inoculation d'extrait de glande de *Liopholidophis lateralis*, (Domergue, 1972:1401).

Dans le domaine des relations entre serpents et venins à Madagascar une observation intéressante a été faite par Groves (1978). Après constatation de la mort d'un *Sanzinia madagascariensis* d'élevage, au zoo de Baltimore, consécutive à l'ingestion d'un *Bufo woodhousei fowleri* cet

auteur obtint en 5 minutes la mort d'un *Leioheterodon madagascariensis*, également d'élevage, après ingestion d'un crapaud de la même espèce. Groves rappelle qu'il n'y a pas de crapaud à Madagascar.

* * *

À l'issue de cette brève revue des Ophidiens de Madagascar où nous avons retrouvé les caractères remarquables de la Flore et de la Faune malgaches avec leur extraordinaire endémisme et les problèmes qu'elles posent au biogéographe, je ne puis que souligner l'importance des lacunes de nos connaissances et l'urgence qu'il y a d'y porter remède. La faune ophidienne malgache est en voie d'extinction rapide. Il s'agit d'une responsabilité internationale car on ne peut reprocher à des hommes qui en sont encore à lutter pour leur survie de ne pas se soucier des forêts et des faunes qu'ils détruisent. Notre responsabilité dans la destruction du monde vivant est collective.

Paris, octobre 1981.

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9.1 LISTE DES OPHIDIENS DE MADAGASCAR (1)

Typhlopidae

Typhlina Wagler, 1830 (2)

- T. bramina (Daudin, 1803) (3)
(+ Typhlops microcephalus Werner, 1909)

Typhlops Oppel, 1811 (2)

- | | |
|------------------------------------|------------------------------------|
| T. albanalis Rendahl, 1918 | T. grandidieri Mocquard, 1905 (4) |
| (+ T. ocularis Parker, 1927) | T. madagascariensis Boettger, 1877 |
| T. arenarius (Grandidier, 1872) | T. mucronatus Boettger, 1880 (4) |
| T. decorsei Mocquard, 1901 | T. reuteri Boettger, 1881 |
| T. domerguei Roux-Estève, 1980 (4) | |

Boidae

Acrantophis Jan, 1860

- A. dumerili Jan, 1860 (5) A. madagascariensis (D. et B., 1844)

Sanzinia Gray, 1849

- S. madagascariensis (Duméril et Bibron, 1844)

(1) d'après Guibé, 1958; Domergue, 1969, 1972; McDowell, 1972; Roux-Estève, 1975, 1980; Hahn, 1980; sauf indication contraire genres et espèces sont endémiques de Madagascar s.s.

(2) genre cosmopolite

(3) espèce cosmopolite

(4) connu par le ou les seuls types

(5) l'espèce type du genre est soulignée

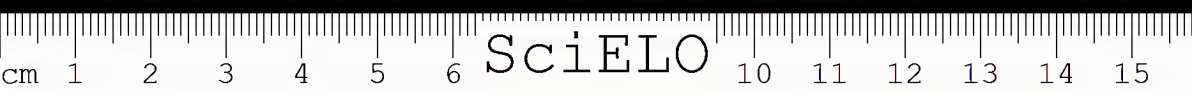
Colubridae

- Alluaudina Mocquard, 1894
A. bellyi Mocquard, 1894 (4) *A. mocquardi* Angel, 1934 (4)
- Compsophis Mocquard, 1898
C. albiventris Mocquard, 1898 (4)
- Dromicodryas Boulenger, 1893 (6)
D. bernieri (D. et B., 1854) *D. quadrilineatus* (D. et B., 1854)
 (+ *Liopholidophis pseudolateralis*
 Guibé, 1956)
- Geodipsas Boulenger, 1896 (6) (7)
G. boulengeri (Peracca, 1892) (4) *G. infralineata* (Günther, 1882)
G. heimi Angel, 1936 (4)
- Heteroliodon Boettger, 1913
H. torquatus Boettger, 1913 (4)
- Ithyocyphus Günther, 1873
I. goudoti (Schlegel, 1837) *I. miniatus* (Schlegel, 1837)
 (+ *I. caudolineatus* Günther, 1873)
- Langaha Lacepède, 1789
L. alluaudi Mocquard, 1901 *L. nasuta* Schaw, 1790
- Leioheterodon Jan, 1863
L. geayi Mocquard, 1905 *L. modestus* (Günther, 1863)
L. madagascariensis (D. et B., 1854)
- Liophidium Boulenger, 1896 (8)
L. rhodogaster (Schlegel, 1837) *L. trilineatum* Boulenger, 1896
L. torquatus (Boulenger, 1888) *L. vaillanti* (Mocquard, 1901)
- Liopholidophis Mocquard, 1904 (6)
L. grandidieri Mocquard, 1904 (4) *L. sexlineatus* (Günther, 1882)
L. lateralis (D. et B., 1854) *L. stumpffi* (Boettger, 1881)
L. pinguis Parker, 1925 (4) *L. thieli* Domergue, 1972
- Lycodryas Günther, 1879 (8)
L. arctifasciatus (D. et B., 1854) *L. guntheri* (Boulenger, 1896)
L. betsileanus (Günther, 1880) *L. inornatus* (Boulenger, 1896) (4)
L. gaimardi (Schlegel, 1837) (9) *L. variabilis* (Boulenger, 1896) (4)
- Madagascarophis Mertens, 1952
M. colubrinus (Schlegel, 1837)
- Micropisthodon Mocquard, 1894
M. ochraceus Mocquard, 1894
- Mimophis Günther, 1868
M. mahfalensis (Grandidier, 1867) (10)
 (= *M. madagascariensis* (Günther, 1868))
- Pararhadinea Boettger, 1898
P. melanogaster Boettger, 1898
- Pseudoxyrhopus Günther, 1881
P. ambreensis Mocquard, 1894 (4) *P. microps* Günther, 1881
P. dubius Mocquard, 1904 *P. occipitalis* Boulenger, 1896
P. heterurus (Jan, 1863) (4) *P. quinquelineatus* (Günther, 1881)
P. imcrinae (Günther, 1890) *P. trilineatus* Mocquard, 1894 (4)

Hydrophiidae

- Pelamis Daudin, 1803 (2)
P. platurus (Linné, 1765) (2)
 (= *Hydrus bicolor* Schneider, 1799)

(6) espèce type non désignée
 (7) genre représenté en Afrique
 (8) genre représenté aux Comores
 (9) Guibé admet une sous-espèce *L.g. granuliceps* (Boettger, 1877)
 (10) Domergue (1968) admet une sous-espèce *lineatus*.



9.3 OPHIDIENS DES COMORES (1)

	Comores s.l.	Grande Comore	Mayotte	Anjouan	Moheji
Typhlopidae					
<i>Typhlina bramina</i> (Daudin, 1803)					
<i>Typhlops comorensis</i> Boulenger, 1889 (+ <i>T. capensis</i> Rendahl, 1918)	+		+	+	+
Colubridae					
<i>Liophidium mayottensis</i> (Peters, 1887)					
<i>Lycodryas maculatus</i> (Günther, 1858)		+	+		+
<i>Lycodryas sanctijohannis</i> (Günther, 1879)		+	+	+	
<i>Lycodryas gaimardi</i> (Schlegel, 1837) (+ <i>L. gaimardi</i> var. <i>comorensis</i> , Peters, 1873)			+		
Hydrophidae					
<i>Pelamis platurus</i> (Linné, 1765)	+	+	+	+	+

(1) d'après Guibé, 1958; Domergue, 1970; Roux-Estève, 1975; Hahn, 1980.

(2) espèce introduite.

(3) présence possible sur les côtes.

(4) Blanc, 1971, donne l'espèce comme présente sur chacune des quatre îles mais sans citer ses sources.

9.4 PARASITES ANIMAUX DES SERPENTS MALGACHES

<i>Parasites</i>	<i>Hôtes</i>	<i>Auteurs</i>
CILIES		
Nyctotherus sp.	Mimophis mahfalensi	Brygoo, 1963
SPOROZOAIRES		
Eimeria sp.	Mimophis mahfalensis, Madagascarophis colubrinus	Brygoo, 1963
Karyolysus sp.	Leioheterodon madagasca- riensis, L. geay, Madagas- carophis colubrinus, Ithycy- phus miniatus, Pseudoxy- rhopus sp.	Brygoo, 1963
Hepatozoon sp.	Acrantophis dumerili, San- zinia madagascariensis	Brygoo, 1963
Hepatozoon domerguei	Leioheterodon modestus, Madagascarophis colubrinus	Landau, Chabaud, Mi- chel et Brygoo, 1970; Landau, 1973
FLAGELLES		
Monocercomonas sp.	Leioheterodon modestus, Madagascarophis colubrinus	Brygoo, 1963
Trypanosoma haranti	Liopholidophis lateralis	Brygoo, 1965
TREMATODES		
Ommatobrephus lobatum madagascariensis	Madagascarophis colubrinus	Richard, 1966
Ommatobrephus pulmo- nicola	Madagascarophis colubrinus	Richard, 1966
CESTODES		
Ophiotaenia ventosalo- culata	Ithycyphus miniatus	Deblock, Rose et Brous- sard, 1962
NEMATODES		
Capillaria madagasca- riensis	Liopholidophis sexlineatus	Ghadirian, 1968
Dioctowittus chabaudi	Leioheterodon modestus	Bain et Ghadirian, 1967
Kalicephalus caryoni	Madagascarophis colubrinus	Ghadirian 1968
K. colubri domerguei	Acrantophis dumerili	—
K. inaequalis	Madagascarophis colubrinus, Ithycyphus miniatus, liop- holidophis lateralis, L. sexlineatus	—
K. paracolubri brygoi	Acrantophis dumerili, San- zinia madagascariensis	—
K. simus mofidii	Leioheterodon madagasca- riensis, L. L. modestus	—
K. viperæ gerhardschadi	Leioheterodon madagasca- riensis, L. L. modestus, L. geayi, Mimophis mahfale- nsis, Madagascarophis colu- brinus, Ithycyphus miniatus	—
Thelandros meridionalis	Acrantophis dumerili	Chabaud et Brygoo, 1962; Brygoo, 1963

Hexametra angusticae- coides	Leioheterodon madagascariensis, Sanzinia madagascariensis, Madagascarophis colubrinus, Acrantophis dumerili	Chabaud et Brygoo, 1960; Ghadirian, 1968
Ophidascaris solenopoion	Ithyeyphus miniatus	Chabaud, 1960
Dracunculus doi	Acrantophis madagascariensis, Sanzinia madagascariensis	Chabaud, 1960; Vaucher et Bain, 1973
Tanqua baina	Sanzinia madagascariensis	Ghadirian, 1968
ACANTHOCEPHALES		
Pseudacantocephalus bigueti	Dromycodryas quadriliniatus	Houin, Golvan et Brygoo, 1965; Golvan, 1969
Pseudoporrorchis rotundatus	Mimophis mahfalensis	Golvan et Brygoo, 1965
PENTASTOMES		
Gigliolella brumpti	Sanzinia madagascariensis, Acrantophis dumerili	Giglioli, 1922; Chabaud et Choquet, 1954; Gretillat, Brygoo et Domerque, 1962; Slocombe et Budd, 1973
Kiricephalus pattoni	Sanzinia madagascariensis, Leioheterodon madagascariensis	Hett, 1924; Heymons et Vitzthum, 1936
Mahafaliella tetrapoda	Acrantophis dumerili	Gretillat, Brygoo et Domerque, 1962
Raillietiella ampanihyensis	Leioheterodon madagascariensis, Madagascarophis colubrinus	Gretillat, Brygoo et Domerque, 1962
ACARIENS		
Hemilaelaps lioheterodon	Leioheterodon modestus	Fain, 1967

LA DÉCOUVERTE DE LA SÉROTHÉRAPIE ANTIVENIMEUSE EN 1894.

PHISALIX ET BERTRAND OU CALMETTE?

Edouard Raoul BRYGOO *

RÉSUMÉ: Après avoir rappelé la découverte de la sérothérapie contre les toxines microbiennes, l'auteur présente de courtes biographies de Phisalix, Calmette et Bertrand avant d'exposer, avec quelques détails, la découverte simultanée des possibilités de la sérothérapie antivenimeuse d'une part par Phisalix et Bertrand au Muséum et de l'autre par Calmette à l'Institut Pasteur. Il décrit la querelle de priorité qui intervint alors avant de citer les travaux de quelques précurseurs et d'exposer comment l'histoire de cette découverte vit dans la mémoire des hommes.

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1. LE CLIMAT SCIENTIFIQUE. LA DÉCOUVERTE DE L'IMMUNITÉ ANTITOXIQUE BACTÉRIENNE. 1890-1894.

Voici cent ans, entre 1880 et 1890, Elie Metchnikoff qui avait, sinon découvert, du moins exposé au monde scientifique le phénomène de la phagocytose, en généralisait le rôle et faisait de cette manifestation cellulaire le support de l'immunité, ce qu'il résumait, dans un livre paru à Londres en 1893, en ces termes:

"The *primum movens* of inflammation consists in a phagocytic reaction on the part of the animal organism. All the other phenomena are merely accessory to this process and may be regarded as means to facilitate the access of phagocytes to the injured part."

Malgré ce remarquable champion, la théorie cellulaire de l'immunité devait alors connaître une importante éclipse avant que les temps modernes ne la réhabilite en partie, par le biais d'autres globules blancs, les lymphocytes, et avec des mécanismes très différents où les "humeurs" jouent un rôle prépondérant. En effet la décennie 1890-1900 fut celle de la victoire des "humoralistes". S'il faut en croire Forster (1970) la théorie humorale de l'immunité eut pour principal pionnier G.H.F. Nuttall qui par sa publication de 1888 établissait l'existence d'un pouvoir bactéricide du sérum à l'égard d'un certain nombre de bactéries, pouvoir détruit par le chauffage du sérum à 55°C. Deux ans plus tard, E. Behring et F. Nissens, alors tous deux assistants de Robert Koch, étendirent cette observation en montrant

- a) que le pouvoir bactéricide du sérum ne s'exerçait pas également à l'égard de toutes les bactéries,
- b) que le sang du rat, animal réfractaire au charbon, avait un pouvoir bactéricide contre l'agent de cette maladie, la bactérie charbonneuse, pouvoir que ne possédait pas celui du cobaye, animal sensible à la maladie.

En août 1890, au Xème Congrès International de Médecine de Berlin, Robert Koch prend nettement position: la phagocytose n'a qu'un rôle accessoire, c'est dans un processus chimique qu'il faut rechercher l'origine de l'immunité. La même année, la théorie humorale de l'immunité recouit une confirmation éclatante avec la publication, le 4 décembre 1890, par Emil von Behring et S. Kitasato de la découverte de l'antitoxine tétanique, ouvrant ainsi une ère nouvelle; c'est une date marquante de l'histoire de la médecine.

Les toxines bactériennes avaient été découvertes l'année précédente d'abord par Emile Roux et Alexandre Yersin pour le bacille de la diphtérie puis par C. Faber pour celui du tétanos. Dans le monde entier des équipes cherchaient le moyen de lutter contre ces deux terribles affections. Le 3

décembre 1890, Carl Fraenkel annonçait l'existence d'une protection de l'animal qui avait été inoculé avec de vieilles cultures chauffées de bacilles diphtériques et le lendemain c'était la publication mémorable de Behring et Kitasato, où, dans une note infrapaginale, le sérum immun est décrit comme "antitoxique". Le 11 décembre 1890, une semaine plus tard, Behring faisait le point sur les possibilités d'immunisation contre la diphtérie. L'équipe allemande avait gagné la course et découvert la possibilité de la sérothérapie. Le mérite principal en revient à Behring mais il convient de lui associer dans notre souvenir les noms de Kitasato qui travaillait avec lui et de Fraenkel qui menait des recherches indépendantes.

Comme toute grande découverte celle-ci fut revendiquée pour des précurseurs et l'on cite le plus souvent, parmi ceux-ci, d'une part Héricourt et Rechet qui, en 1888, avaient mis en évidence une immunité par transfusion péritonéale et d'autre part Babes et Lepp pour des observations au cours de leurs recherches sur la vaccination antirabique.

L'aptitude des organismes vivants de produire des antidotes spécifiques contre les poisons bactériens apparu rapidement comme la manifestation particulière d'un phénomène général, la réponse de l'organisme à la pénétration dans ses humeurs intimes de substances variées. En ce domaine, Paul Ehrlich, créateur de la chimiothérapie, joua un rôle prépondérant en démontrant, dès 1891, soit moins d'un an après la publication de Behring, que l'inoculation de toxines végétales, ricine et abrine, entraînait la production par l'organisme animal d'une antitoxine spécifique. Rapidement il établissait qu'une toxine vieillie, ayant perdu son pouvoir toxique, conservait son aptitude de liaison avec l'antitoxine. Il soulignait également (1892) la différence fondamentale entre immunisation active et immunisation passive.

La publication de la découverte de Behring a tout juste un an lorsque, dans la nuit de Noël 1891, un premier enfant est traité par sérothérapie antidiphtérique par Geissler à la clinique Bergmann de Berlin. Dès l'année suivante commençait en Allemagne la production commerciale d'un sérum antidiphtérique. En 1894, au Congrès de Budapest, Emile Roux et Louis Martin donnent, par la publication de leurs résultats, une grande impulsion à l'utilisation de l'antitoxine chez l'homme. Nuttal (1924) a pu écrire:

"Rarely in the history of scientific discovery have the results of laboratory researches been followed so rapidly by their practical application, and few indeed are the workers in the domain of application of medical science who have in their lifetime seen comparable benefits accrued to mankind as a direct consequence of their labour."

Ce rappel rapide de l'histoire de la découverte des antitoxines bactériennes m'a semblé nécessaire pour comprendre l'ambiance dans laquelle intervient celle des antitoxines et de la sérothérapie antivenimeuse. Alors que la découverte de la sérothérapie antidiphtérique est une magnifique victoire des chercheurs allemands, celle de la sérothérapie antivenimeuse est due à des Français, Césaire Phisalix et Gabriel Bertrand au Muséum d'Histoire Naturelle d'une part et Albert Calmette de l'autre, aux Instituts Pasteur de Saïgon, Paris et Lille.

Qui étaient ces trois hommes ?

2. VIES PARALLÈLES. PHISALIX. CALMETTE. BERTRAND.

Phisalix est le plus âgé des trois hommes dont nous allons étudier la découverte. Fils de cultivateurs, Césaire Auguste Phisalix es né à Mouthiers-Hautepierre (Doubs) en 1852. Il commença des études pour être médecin militaire à Besançon avant de suivre à Paris les cours du Val de Grâce, de 1876 à 1877, à l'époque ou Alphonse Laveran, son aîné de sept ans, y faisait son temps d'agrégation. Il eut pour condisciple Emile Roux. Phisalix, affecté comme médecin militaire à Besançon occupait ses loisirs à des observations d'histoire naturelle, ce qui lui valut un blâme officiel des autorités militaires pour "occupations étrangères à la médecine." En 1881, Phisalix est envoyé en Tunisie d'où il sera rapatrié sanitaire. Au lieu de passer son congé de convalescence à Besançon, il va à Roskoff, où, travaillant au laboratoire maritime, il accumule des éléments pour sa thèse de science. Bien qu'affecté ensuite à Besançon, il vient, en 1882, subir avec succès les épreuves de la licence en sciences naturelles devant la faculté de Paris. A l'occasion d'une affectation à l'hôpital d'Amélie les Bains il poursuit ses recherches pour sa thèse au laboratoire maritime de Banyuls. Placé en situation de non activité il occupe alors les fonctions de préparateur puis de chef de travaux de zoologie et de botanique à la Faculté des Sciences de Besançon. En avril 1884, Phisalix soutient brillamment à Paris une thèse de doctorat en sciences sur *l'Anatomie et la physiologie de la rate chez les Ichthyopsidés*. Sa santé l'obligeant à quitter la carrière militaire, il est nommé au concours, en 1887, professeur suppléant d'histoire naturelle à l'École de Médecine et de Pharmacie de Besançon. L'année suivante, le professeur Chauveau, titulaire de la chaire de Pathologie comparée au Muséum, lui offre d'entrer dans son laboratoire pour remplir les fonctions d'aide naturaliste, en remplacement de Gibier, mis en congé. Il est titularisé dans son emploi le 30 janvier 1892. La même année le titre est transformé en celui d'assistant. En 1897 il sera nommé professeur intérimaire. En 1895 il avait épousé, à Besançon, mademoiselle Marie Picot, qui s'était distinguée à l'École normale supérieure de Sèvres par un goût très vif pour les sciences expérimentales et était devenue agrégée des lycées de jeunes filles. De santé fragile depuis son séjour de Tunisie, Césaire Phisalix mourut le 16 mai 1906. Il est enterré dans son village natal, à Mouthiers.

La liste de ses publications scientifiques, établie par Degrez (1910), comprend 144 titres dont la moitié sont consacrés à l'étude des venins, les autres traitant d'Embryologie, d'Anatomie et Physiologie, de Pathologie générale et de Microbiologie.

La mort prématurée de Césaire Phisalix avait compromis la publication de l'ouvrage qu'il avait projeté d'écrire avec sa femme, devenue sa dévouée collaboratrice. Celle-ci heureusement ne se découragea pas, assumait la totalité de la charge et pût ainsi publier en 1922 la monumentale somme que nous connaissons tous, *Animaux venimeux et venins*. Elle devait, ensuite, jusqu'à l'âge de 85 ans, apporter au laboratoire d'Herpétologie du Muséum la contribution de son activité inlassable et de ses immenses connaissances.

Albert Calmette, né à Nice le 12 juillet 1863 était le cadet de Phisalix de 11 ans. Fils d'un fonctionnaire d'autorité, il souhaitait devenir marin. Ayant dû y renoncer pour raisons de santé il devint médecin de marine. Après plusieurs campagnes lointaines où il était embarqué, il opta en 1890 pour la médecine coloniale. A l'occasion d'un premier stage à l'Institut Pasteur à Paris il fût remarqué par Emile Roux qui le fit désigner par Pasteur pour créer un Institut à Saïgon. De retour en France en 1893, il travailla à l'Institut Pasteur de Paris avant d'être choisi pour fonder un Institut à Lille, où il restera 23 ans, de 1895 à 1919. Il revint ensuite à Paris comme sous-directeur de l'Institut Pasteur, chef du service de la tuberculose et du BCG. Il mourut le 29 octobre 1933, cinq jours avant Monsieur Roux.

Gabriel Bertrand, le plus jeune des trois, était né à Paris le 17 mai 1867. Il avait donc 15 ans de moins que Phisalix et 4 de moins que Calmette. Fils d'un commerçant de la rue Saint Jacques il fréquentait dès l'âge de quinze ans la galerie de Botanique du Muséum où l'accueillait l'aide naturaliste Eugène Poisson. Il s'inscrivit à l'Ecole de la Pharmacie tout en suivant au Muséum les cours de chimie de Fremy. En 1889 il est accueilli dans leur laboratoire par Dehérain et Maquenne et devient en 1890, préparateur chez Arnaud, successeur de Chevreul dans la chaire de Chimie organique du Muséum. Il restera au Muséum jusqu'en 1900, date à laquelle il entre au laboratoire de chimie biologique du Duclaux à l'Institut Pasteur. Il lui succéda en 1904. Pendant son séjour au Muséum il découvrit les oxydases dans le latex de l'arbre à laque, définit les coferments et signala que des caféiers de Madagascar et des Comores ne produisaient pas de caféine. Evoquer la brillante carrière de Gabriel Bertrand après son départ du Muséum sortirait de notre sujet. Il mourut le 20 juin 1962.

3. LA DÉCOUVERTE DE PHISALIX ET BERTRAND. 1894

3.1. L'ambiance.

Phisalix était entré au Muséum d'Histoire naturelle en 1888, comme aide-naturaliste dans le laboratoire de Chauveau. Il y succédait à Gibier. La personnalité d'Auguste Chauveau doit être rapidement évoquée car elle eût une influence directe sur la découverte de Phisalix. Jean Baptiste Auguste Chauveau était né à Villeneuve le Guâard (Yonne) en 1827. Après des études de médecine vétérinaire à Alford et Lyon, il devint directeur de l'école vétérinaire de Lyon, en 1875 puis inspecteur général des services vétérinaires, avant de succéder, en 1886, à Henri Bouley dans la chaire de Pathologie comparée du Muséum.

Bulloch écrit de lui:

"One of the chief French physiologists and pathologists of the nineteenth century." et "a pioneer worker on infective disease." L'influence d'un tel "patron" ne pouvait que marquer Phisalix qui le reconnaît d'ailleurs lui-même (1897:61):

“... j’ai continué la poursuite des recherches que j’avais entreprise sur les venins, avec cette idée directrice inspirée par les travaux de M. Chauveau sur les poisons solubles des microbes que les sécrétions cellulaires toxiques offrent la plus grande analogie avec les sécrétions microbiennes et que les procédés d’atténuation et de vaccination applicables aux unes le sont aussi aux autres.”

3.2. Premiers travaux sur les venins. 1889.

Phisalix commence ses travaux sur les venins par une série d’expériences sur le venin de la salamandre terrestre qui l’amène à publier quatre notes, de 1889 à 1891, dont une avec P. Langlois et l’autre avec Ch. Coutejean. Les débuts de sa collaboration avec Gabriel Bertrand, alors préparateur dans la chaire de chimie organique du Muséum, sont présentés par Phisalix lui-même (1897 :6 1) en ces termes:

“C’est en 1893, qu’avec la collaboration éclairée de mon ami G. Bertrand, j’ai été arrivé à donner aux idées précédentes la sanction expérimentale.”

Il faisait référence à l’idée de l’analogie entre sécrétions cellulaires toxiques et sécrétions microbiennes qu’il devait à M. Chauveau. En 1893 et 1894, Phisalix et Bertrand publient d’abord trois notes sur la toxicité du sang et du venin de crapaud et de vipère, sur l’immunité naturelle au venin de vipère et sur les glandes venimeuses chez les couleuvres, avant d’en arriver à la publication de leur découverte.

3.3. La découverte. 10 février 1894.

L’originalité de la découverte de Phisalix et Bertrand est toute entière exposée dans la note qu’ils présentèrent le 10 février 1894 à la Société de Biologie de Paris sous le titre:

“Sur la propriété antitoxique du sang des animaux vaccinés contre le venin de vipère.”

Après avoir exposé leurs expériences: le sérum des cobayes, prélevé 48 heures après l’inoculation immunisante d’échidno-vaccin, défibriné, puis mélangé avec le venin et injecté dans le péritoine d’autres cobayes, les rend capables de résister à l’action mortelle du venin; ils concluent:

“... la puissance antitoxique du sang est susceptible d’être augmentée dans des proportions considérables... nous espérons obtenir des modifications du sang suffisamment intenses pour qu’il puisse être utilisé comme agent curatif.”

Dans un autre article, de la même année, ils expliquent bien l’origine de leur découverte:

“L’étude des venins est entrée dans une voie nouvelle depuis que la notion des poisons solubles d’origine microbienne a été introduite en physiologie par M. Chauveau.” et : “Notre travail avait pour point de départ la comparaison des venins de vipères avec les toxines microbiennes; nous venons de démontrer la ressemblance en ce qui concerne l’atténuation par la chaleur et la transformation de ce venin en vaccin.”



3.3. Les conditions de la découverte

Lorsque l'on analyse les protocoles expérimentaux de Phisalix et Bertrand, on ne peut s'empêcher de sentiments mêlés d'une part devant la pauvreté, la parcimonie des moyens mis en oeuvre et d'autre part la richesse de l'exploitation des observations et la hardiesse des conclusions. Ils ne travaillaient que sur un très petit nombre d'animaux, avec une dose d'épreuve limitée à une dose minima mortelle et peu ou pas de témoins. Qu'ils aient pu, dans ces conditions, aboutir à leur découverte est la preuve manifeste de leurs talents d'expérimentateurs. (1)

Mais ces conditions expérimentales étaient aussi favorables à l'interférence de phénomènes "parasites" qu'ils pouvaient d'autant moins détecter qu'ils défrichaient une terre nouvelle pour la science. C'est sans doute à ces conditions très particulières que l'on doit de leur avoir vu décrire, entre 1895 et 1898 une action vaccinnante contre le venin de vipère chez une série de substances variées : le sérum des espèces douées d'immunité naturelle, vipère, couleuvre, hérisson, anguille sous réserve de le chauffer pendant 15 minute à 58°C pour en détruire l'action toxique "phlogogène"; le sérum d'espèces sensibles comme le cobaye et le cheval; la sécrétion cutanée muqueuse de la grande salamandre du Japon; diverses sécrétions muqueuses, venimeuses ou non; le venin des vespides; la bile; la tyrosine; le suc de tubercule de dahlia; le suc de divers champignons.

L'immunologie était en gestation, la notion de spécificité des réactions n'était pas encore établie. Phisalix et Bertrand étant convaincus (1896) que la substance vaccinnante était fondamentalement différente de la substance toxique, in n'était pour eux, paz étonnant de la retrouver seule, dans des organismes divers, sans rapport avec la toxine elle même.

Nous venons de voir ce qu'avait découvert l'équipe qui travaillait au Muséum d'histoire naturelle dans le laboratoire de Chauveau. Qu'en était-il à L'Institut Pasteur?

4. LA DÉCOUVERTE D'ALBERT CALMETTE. 1894

4.1. Premiers contacts avec le venins.

Albert Calmette n'était à Saïgon que depuis neuf mois lorsqu'il recut, en octobre 1881, un télégramme de l'administrateur de Bac Lieu, signalant qu'il disposait de 19 cobras capturés par un Annamite "moitié psyllle moitié sorcier" lors d'une inondation et proposant l'envoi au laboratoire des serpents et de leur maitre. Et dans une lettre à son père du 7 novembre 1891 (2) où Calmette raconte ces faits, de préciser:

"J'ai accepté ... Je l'emploie (le venin) à des expériences dont l'intérêt est très grand parce que jamais une étude aussi complète du venin n'a pu être tentée dans des conditions favorables."

(1) Un autre point mériterait sans doute vérification. Phisalix et Bertrand, dans leur publication de 1894, signalent observer l'apparition des propriétés immunitaires transférables quarante-huit heures après l'inoculation de l'échidovaccin! S'agissait-il vraiment du même phénomène que celui décrit par Calmette? Les auteurs en étaient persuadés.

(2) Cité par N. Bernard, 1961 : 79.

C'était l'exploitation scientifique par un chercheur doué et bien formé d'une "oopportunité", comme l'on dit aujourd'hui, d'une occasion, dont seuls certains êtres savent tirer profit.

Il s'appliqua d'abord à déterminer chez divers animaux les effets physiologiques du venin puis, rapidement, hanté qu'il était par une analogie probable entre les propriétés des venins et celles des toxines microbiennes (N. Bernard, 1961:86) il étudia l'action de divers produits chimiques capables de donner avec les venins des précipités insolubles dans l'eau et dans les humeurs, donc de les neutraliser. Il en expérimenta une trentaine avant de sélectionner le chlorure d'or et els hypochlorites alcalins. Le premier animal vacciné qu'il obtint à Saïgon, en 1892 fut une poule.

Revenu de Saïgon le 21 juillet 1893, Calmette reprend dès le mois d'octobre, auprès de Monsieur Roux, ses recherches sur le venin de cobra qui devaient le conduire à la découverte de la sérothérapie et qui avaient déjà fait l'objet d'un travail publié aux *Annales de l'Institut Pasteur* en 1892. C'était sa première note sur les venins. Depuis trois ans déjà Phisalix publiait sur ce sujet.

4.2. Mise au point d'une vaccination. Production d'un antiserum.

Calmette travaillait avec du venin de cobra, beaucoup plus toxique que celui de vipère et difficilement atténuable par la chaleur. Il fût donc obligé de mettre au point des techniques de vaccination beaucoup plus rigoureuses.

La première annonce d'un sérum à activité thérapeutique est fait par Calmette à la séance de la Société de Biologie du 10 février 1894, celle là même où Phisalix et Bertrand venaient d'exposer leurs propres résultats. Sa note avait pour titre:

"L'immunisation artificielle des animaux contre le venin des serpents et la thérapeutique expérimentale des morsures venimeuses."

Calmette commence par exposer trois techniques possibles de vaccination avant d'écrire:

"Dans tous les cas, et quelle que soit la méthode employée, l'immunisation n'est jamais réalisée avant un minimum de trois semaines, et elle ne se produit qu'à condition que l'animal ait été malade."

Puis il passe aux développements possibles de sa découverte:

"... ce sérum était également thérapeutique: mes expériences sur l'animal m'autorisent à espérer beaucoup pour l'application à l'homme... L'expérimentation sur l'animal nous fait donc concevoir l'espérance que l'on pourra traiter avec succès les personnes mordues, d'abord par des injections d'hypochlorites alcalins autour de l'inoculation venimeuse, et ensuite par des injections de sérum thérapeutique qui entraveront les phénomènes généraux produits dans l'organisme par l'envenimation ophidienne".



4.3. Le faire savoir.

Alors que Phisalix et Bertrand étaient tout aussi convaincus que Calmette de l'importance de leur découverte et des conséquences heureuses qu'elle pouvait avoir pour la protection des hommes, seul ce dernier su mettre en oeuvre les moyens pour la faire connaître.

En 1896, en même temps qu'il publiait à Paris son ouvrage sur le venin des serpents, Calmette donnait au *British medical Journal* un article sur la mesure du pouvoir antitoxique des sérums antivenimeux. La même année, au mois de juillet, devant une commission du *Royal College of Physicians and Surgeons* de Londres il effectuait une démonstration de l'action du sérum qui entraînait l'adhésion complète des assistants et la rédaction d'un procès verbal recommandant, sans restriction, l'utilisation de la sérothérapie dans le traitement des morsures venimeuses de serpents. L'année suivant, il rédigeait le chapitre *The Snakes Venoms*, dans le traité de Clifford Albutt, *Infectious Diseases Pathology*. Par la suite, ses contributions à différentes publications étrangères: en allemand, 1905, 1907, 1908, 1910 et 1915, dont les chapitres sur Venins et animaux venimeux des deux traités magistraux de Kolle et Wasserman, *Handbuch der pathogenen Mikroorganismen* et de Mense, *Handbuch der tropenkrankheiten*; et en anglais, avec la publication en 1908 de la traduction de son ouvrage magistral sur "les Venins, les animaux venimeux et la sérothérapie antivenimeuse" puis, en 1909, un article dans le *Journal of medical Research de Boston*, contribuèrent à universaliser la connaissance de sa découverte.

5. QUERELLE POUR UNE PRIORITÉ

Comme beaucoup de découvertes importantes, celle de la sérothérapie antivenimeuse eut droit à sa querelle de priorité qui prit d'autant plus de relief que les adversaires travaillaient les uns et les autres à Paris et utilisaient les mêmes moyens de diffusion. L'action se passe pendant le premier semestre 1894 et est toute entière exposée dans le volume 46 des Comptes rendus de la Société de Biologie et dans le volume 118 de ceux de l'Académie des Sciences. Dans deux notes, présentées par Chauveau aux séances de l'Académie des 5 et 12 février, Phisalix annonçaient leur découverte. Dans la première "Atténuation du venin de vipère par la chaleur et vaccination du cobaye contre ce venin", ils font référence, en note infrapaginale, à un travail de Calmette, de 1892, sur l'atténuation du venin de cobra par la chaleur; dans la seconde "Sur la propriété antitoxique du sang des animaux vaccinés contre le venin de vipère." Ils écrivent: "..., nous espérons obtenir des modifications du sang suffisamment intenses pour qu'il puisse être utilisé comme agent thérapeutique."

Un mois plus tard, à la séance du 27 mars, est présentée la note Calmette: "Propriétés du sérum des animaux immunisés contre le venin des serpents; thérapeutique de l'envenimation." où l'auteur écrit:

“Le sérum des animaux ainsi traités est à la fois *préventif*, *antitoxique* et *thérapeutique*, exactement comme celui des animaux immunisés contre la diphtérie et le tétanos.” Ajoutant, ce qui est aujourd’hui reconnu inexact, :

“Il possède ces propriétés, non seulement à l’égard du venin qui a servi à immuniser l’animal dont on l’a retiré, mais même à l’égard de venins d’autres origines.” Le sérum de lapin immunisé contre le venin de cobra, par exemple, est antitoxique à l’égard des venins de *vipère* de France, *d’hoplocephalus* et de *pseudechis* d’Australie.” Il ne signalait aucun travail sur ce sujet antérieur au sien.

Dès le mois suivant, à la séance du 23 avril, réaction de Phisalix et Bertrand, :

“Observations à propos de la note de M. Calmette relative au venin des serpents.” avec conclusion :

“... M. Calmette ayant omis de citer nos recherches, nous sommes dans l’obligation d’en rappeler l’antériorité, car nous pensons que des conséquences théoriques et pratiques importantes découleront logiquement des faits que nous avons scientifiquement établis.”

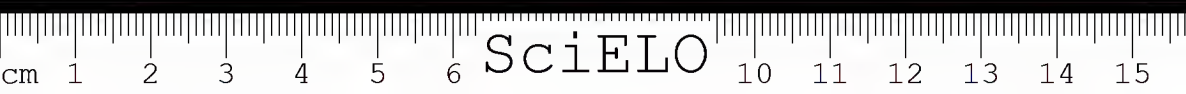
M. Chauveau, qui avait présenté cette note ajoutait, en remarque que M. Kaufmann avait, dès 1888, signalé la possibilité d’immuniser l’animal par injections répétées de petites quantité de venin entier.

La querelle aurait dû en rester là. Mais la semaine suivante, le 30 avril, Calmette dans une note présentée par Duclaux et intitulée “Propriétés du sérum des animaux immunisés contre les venins de diverses espèces de serpents.” revendique la priorité car la note par laquelle Phisalix et Bertrand annonce la possibilité d’une sérothérapie n’est que du 12 février,

“Or, le 10 février, deux jours avant la deuxième note de MM. Phisalix et Bertrand, j’avais communiqué à la Société de Biologie les résultats non seulement encourageants, mais *positifs*, de *prévention* et de *thérapeutique* de l’envenimation que j’obtenais avec des sérums d’animaux immunisés. La priorité, en ce qui concerne la détermination des pouvoirs antitoxique, préventif et thérapeutique des sérums d’animaux immunisés contre le venin, m’appartient incontestablement.”

Réponse, la semaine suivante, de Phisalix et Bertrand: “Sur la réclamation de M. Calmette à propos du sang antitoxique des animaux immunisés contre le venin des serpents.” où ils expliquent: “la note que nous avons présentée le 12 février à l’Académie est exactement la même que celle que nous avons communiquée à la Société de Biologie le 10 février, dans la séance où M. Calmette a lu la sienne, avant même qu’il eût pris la parole. Au Bulletin de la *Société de Biologie* (16 février 1894, n.º 5), notre note, page 111, est la première en tête du numéro où celle de M. Calmette vient à la page 120.”

Même s’il ne s’en fallait que de très peu, Phisalix et Bertrand étaient manifestement gagnants, aussi bien à la Société de Biologie qu’à l’Académie des Sciences tandis que Calmette ne se montrait vraiment



pas beau joueur (3). Eut-il simplement cité les deux autres auteurs dans sa première note à l'Académie, que sa gloire n'en aurait rien perdu et qu'une pénible querelle eut peut être été évitée. Mais tandis que la polémique sur la priorité de la découverte de la sérothérapie se déroulait devant l'Académie des Sciences une autre divergence opposait les mêmes auteurs devant la Société de Biologie. Dans sa note du 10 février 1894, Calmette, avant d'en venir à la thérapeutique des morsures, s'étonnait des résultats de Phisalix et Bertrand qui réussissaient à atténuer le venin de vipère par la chaleur alors que lui-même échouait avec ce procédé. Phisalix et Bertrand répondaient dans une note insérée à la suite de celle de Calmette, estimant que des conditions expérimentales différentes pouvaient rendre compte des différences de résultats observées. A la séance de la Société de Biologie du 3 mars 1894, Calmette donna une nouvelle note signalant des expériences effectuées en commun avec Phisalix et Bertrand et concluant:

"La divergence de nos résultats s'explique par la différence de toxicité qui existe entre les venins que nous employons."

L'année suivante ces chercheurs s'opposèrent encore, mais sur une autre question, à propos de l'action de l'hypochlorite de soude. Calmette (1894) y voyait un moyen majeur de lutter contre l'envenimation, de plus, dans une autre note il faisait état d'un résultat pour le moins curieux qui montre que les idées sur les actions spécifiques n'étaient pas encore fixées:

"C'est ainsi qu'il suffit d'injecter pendant quatre ou cinq jours de suite à des lapins, sous la peau, une dose de 6 à 8 centimètres cubes d'une solution d'hypochlorite de chaux au 1/60e, pour rendre ces animaux tout à fait réfractaires à l'inoculation d'une dose deux fois mortelle de venin."

En 1895, relevant que Calmette semble admettre que l'hypochlorite aurait la propriété "de produire la même réaction vaccinale que le venin chauffé" Phisalix et Bertrand écrivent "on comprendra quelle valeur théorique et pratique aurait la découverte de M. Calmette, si elle était confirmée. Malheureusement, les recherches que nous avons entreprises dans ce but conduisent à des conclusions opposées." et plus loin:

"Ceci démontre bien, contrairement à ce qui est avancé par M. Calmette, que l'hypochlorite de calcium ne protège pas l'organisme en y provoquant la formation d'une substance antivenimeuse, ni, non plus,

(3) Cet aspect particulier de son caractère se retrouve lorsqu'en 1907 il écrit:

"La sérothérapie antivenimeuse que mes travaux, complétés par ceux de Phisalix et Bertrand, de Frasser, de Géo Lamb, de F. Tidwell, de Mac Farland et de Vital Brazill ont permis d'établir sur des bases scientifiques, est maintenant entrée dans la pratique médicale courante."

C'était vraiment ne pas être régulier que de ne pas reconnaître la simultanéité des recherches de Phisalix et Bertrand et des siennes et de les mettre sur le même plan que celle des chercheurs ultérieurs; la liste est d'ailleurs incomplète car les travaux de Flexner et de Noguchi ont précédé ceux de Lamb et de Vital Brazill. A noter qu'en 1896 il avait été plus "correct" en écrivant:

"A partir de 1894, les recherches poursuivies simultanément : au Muséum d'histoire naturelle de Paris, par Phisalix et Bertrand, sur le venin de Vipère; à l'Institut Pasteur de Paris, par moi-même, sur le venin de Cobra, puis sur d'autres venins de diverses origines, aboutissent à des résultats beaucoup plus précis."

comme cet auteur en a émis l'invraisemblable hypothèse, en pénétrant dans la circulation et y persistant, pour y détruire le venin comme il le ferait dans un verre à expériences."

Calmette ne revint plus sur l'action vaccinnante de l'hypochlorite, mais en 1907 il écrivait encore:

"L'hypochlorite de chaux ... détruit sûrement et immédiatement le venin par simple contact et, en raison de la grande diffusibilité du chlore gazeux qu'il dégage, ce dernier agit à distance, assez loin du point d'inoculation, sur le venin qui commence à être déjà absorbé."

C'était vraiment une affirmation audacieuse, même remise dans le contexte des connaissances des années 1900. Calmette n'était manifestement pas un physiologiste.

Cette combativité entre deux équipes de chercheurs parisiens traduit l'émulation existante alors entre l'Institut Pasteur d'une part et le Muséum de l'autre, le premier représenté par Roux, son directeur, héritier spirituel de Pasteur et patron direct de Calmette, le second par Chauveau, maître de Phisalix, microbiologiste de grande renommée lui aussi, mais n'appartenant pas à la mouvance de Pasteur.

6. LES PRÉCURSEURS

Ainsi, Phisalix et Bertrand d'une part et Calmette de l'autre, avaient simultanément en 1894 découvert la possibilité de la sérothérapie antivenimeuse. Mais la querelle de priorité que nous venons d'évoquer ne saurait nous faire oublier l'existence de précurseurs, car, comme toute découverte, celle-ci fût préparée par des observations et expérimentations qui à vrai dire concernaient surtout les possibilités d'immuniser les animaux contre les venins.

L'histoire a retenu trois noms, celui d'un italien Domenico Fornara, d'un américain H. Sewall et d'un français, M. Kaufmann.

Le premier, en 1877, étudiant les effets physiologiques du venin de Crotale, par des inoculations successives obtint la résistance du chien contre ce venin. Sewall, professeur à l'Université de Michigan, dix ans après, dans un important travail sur le venin de Crotale, avait montré qu'on peut rendre les pigeons graduellement plus résistants à l'action de ce venin en leur injectant d'abord des doses très petites. Kaufmann enfin, professeur de physiologie à l'école vétérinaire d'Alfort, est celui qui, à partir de 1889, consacra le plus de travaux à ce sujet. (4) En 1889, il pouvait écrire:

"Il semble que des inoculations successives de faibles doses de venin communiquent une certaine immunité contre des doses fortes."

Il avait expérimenté avec du venin de *Vipera aspic* sur des cobayes. Il poursuivit ses expériences et quatre ans plus tard (1893 : 136) publiait ses observations faites sur une chienne de 1890 à 1892 pour conclure:

(4) En 1901, une trousse du professeur Kaufmann contre les morsures de vipères était encore commercialisée.



“Les observations faites sur cette chienne m’ont appris que des inoculations successives de petites quantités de venin peuvent communiquer une résistance plus grande au venin, mais qu’elles sont incapables de conférer une véritable immunité contre l’envenimation.” (5)

Dans une note présentée à la séance de la Société de Biologie du 10 février 1894 et qui, dans les Comptes Rendus, fait immédiatement suite à celle de Phisalix et Bertrand, Kaufmann, après avoir rappelé les résultats qu’il a publiés, peut légitimement écrire:

“Les recherches de MM. Phisalix et Bertrand confirment donc les conclusions que j’avais déjà formulées et qui étaient basées sur des faits expérimentaux obtenus par un procédé différent.”

Ces “précurseurs” n’avaient, en fait, qu’appliqué à leurs animaux une méthode de mithridadisation dont le nom seul évoque qu’elle appartient au patrimoine commun de l’humanité. Il n’était question pour eux ni de modifier le venin avant de l’injecter ni encore moins de chercher à obtenir un antidote utilisable chez d’autres sujets. Phisalix et Bertrand, Calmette, avaient donc bien découvert quelque chose de nouveau. Mais qu’en pensaient leurs contemporains?

7. COMMENT FÛT REÇU LA DÉCOUVERTE ET COMMENT ELLE VIT DANS LA MÉMOIRE DES HOMMES.

7.1 Les contemporains.

Les contemporains reconnaissent sans conteste l’importance de la découverte de Phisalix et Bertrand puisque ceux-ci obtinrent l’année même où ils la firent, en 1894, le prix Monthyon de l’Académie des Sciences pour la découverte d’un sérum antivenimeux. (6) En 1898, Césaire Phisalix obtenait, sur rapport du professeur Bouchard, le Prix Bréhant, de l’Académie des Sciences pour l’ensemble de ses travaux sur les venins et les animaux venimeux. Un an après la publication des premiers résultats, T. R. Fraser, en Angleterre, les confirmait en présentant devant la société médico-chirurgicale d’Edimbourg un lapin vacciné contre une dose de venin de Cobra cinquante fois mortelle. Emile Roux, à propos des recherches de Calmette sur les venins écrivait:

“L’impulsion qu’il leur a donnée a été féconde en résultats pratiques et en acquisitions d’un grand intérêt scientifique.” (7) En 1922, Laveran, autre autorité scientifique non contestée, écrivait:

(5) Les intéressantes observations de Kaufmann furent le plus souvent citées de manière inexacte: si Calmette (1907: 253) donne correctement le résultat et la date de 1889 il n’y a, comme référence, que le livre de 1893; Mme Phisalix (1922: 759) ne fait état que de l’expérience sur le chien, avec sa date exacte (1893) mais ne donne dans sa bibliographie qu’une référence de 1894; P. Boquet (1948: 111; 1970: 640) cite le nom de Kaufmann sans précision ni référence en 1948 et avec une référence erronée en 1970.

(6) Ce qui était une manière pour les Académiciens de faire connaître leur jugement sur la querelle de priorité à laquelle ils venaient d’assister.

(7) cité par N. Bernard (1961: 78-79) sans indication d’origine.

“Ces découvertes (celles de Phisalix et Bertrand et de Calmette), qui remontent à 1894 ont eu, comme on le sait, les résultats les plus heureux au point de vue de la sérothérapie antivenimeuse, qu’elles ont inaugurée.”

7.2 Les modernes.

Un certain nombre d’auteurs modernes, historiens des sciences, ignorent aussi bien Calmette que Phisalix et Bertrand. C’est le cas de Taylor (1963) dans son Histoire illustrée de la Biologie et de Williams (1969) dans son Dictionnaire biographique des savants. L’ouvrage de la Behringwerk (1963) sur les serpents venimeux, ne mentionne que Calmette dans son introduction. Pour beaucoup, Calmette est le seul inventeur de la sérothérapie antivenimeuse. Il est certain que le retentissement des démonstrations publiques en leur temps, puis celui de la publication de son ouvrage et, peut-être surtout, de sa traduction anglaise firent beaucoup pour établir dans l’esprit du public le rôle de Calmette. Pour Grainger (1958), Calmette est le:

“Discoverer of the antivenin serum and the BCG vaccine”, sans un mot de Phisalix ni de Bertrand. La paternité unique de la découverte lui est également attribuée par Delaunay (1962). Il s’agit là de deux historiens bactériologistes, beaucoup moins acceptable est l’erreur d’auteurs herpétologistes comme Ditmars (1969):

“The discovery of antivenin, by Dr. Albert Calmette, of the Pasteur Institute...” ou comme Klobusitzky (1971):

“Calmette (1894) the founder of serum therapy against snake bites.”

Un cas particulier mérite d’être mentionné, celui des historiographes de Calmette. Alors qu’en 1939 Bernard et Nègre écrivaient:

“Les découvertes simultanées de l’immunisation par des procédés différents, contre le venin de *Vipera berus* par MM. C. Phisalix et G. Bertrand et contre le venin de *Cobra* par A. Calmette, et leur publication au cours d’une même semaine apportaient le principe du traitement spécifique de l’envenimation par des sérums thérapeutiques.” En 1961, le même Noël Bernard; présentant la vie et l’oeuvre d’Albert Calmette “sur un plan et sous une forme différente”, ne cite plus Phisalix et Bertrand qu’à l’occasion de l’immunité du hérisson, attribuant de ce fait toute la paternité de la découverte de la sérothérapie à Calmette.

Si pour beaucoup les noms de Phisalix et de Bertrand n’ont pas paru dignes d’être conservés, cet oubli n’est heureusement pas général et quelques auteurs français leur rendent un équitable hommage:

Charles Joyeux (1944): “Le sérum antivenimeux a été découvert simultanément par Phisalix et Bertrand, et par Calmette (1894).”

Paul Boquet (1948): “Enfin, quatre ans après la découverte des anti-toxines par Behring, C. Phisalix avec G. Bertrand, et, indépendamment,

A. Calmette, obtiennent chez le cobaye et le lapin un sérum spécifique capable de neutraliser les venins de serpents." (8)

7.3 Mais qu'en est-il au Muséum d'Histoire naturelle?

Edmond Perrier, alors directeur du Muséum, à l'occasion de la levée du corps de Césaire Phisalix à la gare de Lyon en 1906, lui rendait hommage: "il trouva le moyen de neutraliser plusieurs d'entre eux (venins) et peut disputer à Calmette, qu'il semble bien avoir devancé d'ailleurs, l'honneur d'avoir trouvé un puissant antidote contre les venins des serpents les plus redoutables."

Et au laboratoire d'Herpétologie (9) qu'hante encore l'ombre de Mme Phisalix, la tradition orale conserve la notion de la découverte au Muséum du sérum antivenimeux et le nom de ses auteurs, mais ailleurs, dans la Maison?

Dans l'historique de l'activité du Muséum que donna, en 1935, Paul Lemoine, à l'occasion du tricentenaire de sa fondation, il est tout à fait remarquable que pas un mot ne mentionne la découverte dans l'établissement de la sérothérapie antivenimeuse alors que Phisalix et Bertrand y sont cités, le premier comme aide naturaliste puis professeur intérimaire, le second pour avoir "découvert au Muséum la Laccase, les oxydases puis les conferments". L'oubli n'est heureusement pas total puisque l'on peut trouver, en 1954 (10), sous la plume de Roger Heim les lignes suivantes:

"Avec C. Phisalix, à qui le lia une profonde amitié, trop tôt interrompue par la mort de celui-ci, Gabriel Bertrand entreprend une série remarquable de travaux qui conduiront à la découverte de la vaccination antivenimeuse. Il n'a pas cessé de s'intéresser à ces problèmes depuis."

Madame Phisalix (1940 a donné une explication intéressante du fait que la découverte au Muséum du sérum antivenimeux était restée sans lendemain:

"Le sérum contre le venin de Vipère, le premier des sérums antivenimeux découvert n'est cependant pas celui qui, le premier, a passé dans la pratique courante, car le Muséum d'Histoire naturelle, au temps même ou, Jardin du Roy, il avait sa pharmacopée particulière, n'a jamais délivré en ce temps au public les "remèdes exquis", c'est-à-dire souverains que Moyse Charas avait retirés de la Vipère et préparés contre ses morsures. Ces remèdes étaient réservés au Roy, à sa maison, et aux officiers de sa maison, les professeurs d'alors. On se souvient que Vallot, premier médecin du Roy et surintendant du jardin, appelé *in extremis* auprès de la Duchesse d'Orléans, Madame, qui se disait empoisonnée, lui administra, d'ailleurs sans succès, de la Poudre de Vipère délayée dans de l'huile d'olive. Les traditions de la Maison, sous ce rapport, n'ont pas changé."

(8) Cette phrase se trouve dans l'historique, à la page 14, ce qui n'empêche pas Boquet, à la page 111 d'attribuer au seul Calmette, et à une date erronée (1896), la démonstration que le sérum des animaux prémunis contient des antitoxines spécifiques ! Les mêmes erreurs se retrouvent dans son travail de 1970.

(9) Le laboratoire le plus voisin de celui où Phisalix et Bertrand effectuèrent leur découverte.

(10) Dans un article consacré à G. Bertrand.

Je laisse à Madame Phisalix la responsabilité de cette explication "historique" de la non exploitation d'une découverte faite au Muséum. En ce qui concerne l'oubli du fait lui-même, alors qu'il n'a pas cent ans, il me semble que l'on peut y trouver plusieurs explications. Il y a d'abord la mort précoce du principal auteur, Césaire Phisalix qui n'était plus là pour défendre ses droits, il y a ensuite le changement d'orientation des recherches de Gabriel Bertrand qui s'éloigna du Muséum, et des venins, il y a surtout la disparition du laboratoire où avait été effectuée la découverte. La chaire de Pathologie comparée à laquelle appartenait Phisalix fût en effet, en 1917, transformée en Chaire des Vers et Crustacés, tandis que les locaux quelle occupait, construit par Chauveau, était affectés à la chaire de Physiologie générale et comparée. Et celle-ci n'hérita pas des traditions et souvenirs de la chaire disparue puisque Maurice Fontaine, faisant en 1944, dans sa leçon inaugurale, l'historique de la chaire de Physiologie générale et comparée pouvait légitimement ne pas compter au nombre des recherches et découvertes de ses prédécesseurs, les travaux de Chauveau et ceux de Phisalix, tout en rendant hommage au premier pour avoir su doter le Muséum d'un grand laboratoire de physiologie.

8. EN GUISE DE CONCLUSION.

Il me semblerait logique de demander à Madame Phisalix un jugement équitable. Elle ne peut être suspecté de prévention contre les travaux d'un mari qu'elle admirait, elle était de surcroit particulièrement experte en matière de venins et d'animaux venimeux. Pour elle

- à Phisalix et Bertrand, au Muséum, en 1894, la première observation sur les propriétés antivenimeuses du sang des animaux vaccinés ou moyen du venin de Vipère et la découverte de la sérothérapie;
- à Calmette, en 1896, à l'Institut Pasteur de Lille, la préparation du premier sérum antivenimeux délivré au public contre la morsure du Cobra de l'Inde.

Tel est son jugement, pouvons nous le faire notre?

Il me semble trop sévère et ne pas rendre pleine justice à Calmette qui avait bien, dès 1894, et indépendamment, découvert la sérothérapie antivenimeuse; le reconnaître ne diminue en rien les mérites de Phisalix et Bertrand.

—ooOoo—

Peut-être n'était-il pas inutile de rappeler les origines d'une découverte qui connut un si grand développement et dont le rayonnement dans le monde fut particulièrement rapide avec l'apparition des nombreux instituts spécialisés dans la préparation des sérums antivenimeux et dont l'un des plus célèbres est, sans conteste, celui de Butantan, fondé voici quatre vingt ans, en 1901, par le Dr. Vital Brazil. (11)

(11) Parmi les premiers fondés on peut citer, celui d'Australie, à Sydney par F. Tidswell, aux Indes ceux de Kasauli et Bombay par Géc. Lamb et Semple et aux Etats Unis, à Philadelphie, celui de J. Mac Farland.

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SciELO

LES SPÉCIMENS-TYPES DU GENRE *MICRURUS* (ELAPIDAE) CONSERVÉS AU MUSÉUM NATIONAL D'HISTOIRE NATURELLE DE PARIS

Rolande ROUX — ESTEVE *

Les collections herpétologiques du Muséum National d'Histoire Naturelle de Paris renferment un grand nombre de spécimens-types en particulier ceux qui correspondent aux descriptions figurant dans l'*Erpétologie Générale* de Duméril, Bibron et Duméril (1834-1854), oeuvre considérable composée de 9 tomes (en réalité, 10 volumes, puisque le tome VII des Ophidiens comporte 2 fascicules).

A côté des spécimens, vus et étudiés par les Duméril et Bibron, dont près de 85% sont encore dans nos collections, nous trouvons quelques types, peu nombreux, de leurs prédécesseurs, tels Lacépède, Cuvier, Daudin; ainsi que de leurs contemporains, tels Schlegel, un de leurs principaux correspondants, Schweigger, élève assidu des cours de Constant Duméril qui s'est illustré dans l'étude des Chéloniens; Lesson, Lesueur pour ne citer que ces derniers parmi les voyageurs célèbres du début du XIX^{ème} siècle.

Après la mort de Bibron (1848) et quelque peu avant celle de Constant Duméril (1860), le fils de ce dernier, Auguste, aidé de Séraphin Braconnier, son préparateur, fit parvenir en 1857, à Jan, le célèbre Ophiologiste de Milan, une grande partie de nos spécimens types et non-types, pour l'élaboration de l'*Iconographie Générale des Ophidiens*, oeuvre colossale et d'une étonnante rigueur scientifique. Chaque spécimen est, quand sa taille l'a permis, représenté en vraie grandeur avec tous les détails d'écaillure, les anomalies individuelles et la coloration que l'on peut observer, encore à l'heure actuelle.

Jan a donc, à cette époque, réexaminé tous les spécimens envoyés et, quand cela lui est apparu nécessaire, les a redécrits et les a fait figurer par Sordelli, son collaborateur, sous un nouveau nom avant de les renvoyer à Paris. Ce qui explique la présence d'une partie non négligeable de spécimens-types de Jan dans nos collections.

Depuis cette époque, le nombre de types n'a cessé de s'accroître et il est parfois regrettable de constater que certains herpétologistes, français ou non, négligent d'avoir recours aux types du Muséum de Paris lorsqu'ils font des révisions de famille ou de genres.

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C'est pourquoi, je me suis permis, à l'occasion de ce Symposium de faire l'inventaire des spécimens-types du genre *Micrurus*.

J'indique pour chaque spécimen son numéro de collection (1) et les caractères qui me semblent les plus utiles à une étude ultérieure: mensurations, écaillure, coloration et la synonymie.

J'ajouterai une remarque au sujet des Elapidés et de leur importance dans l'Erpétologie Générale:

Les différents tomes ne se sont pas succédés dans le temps en suivant l'ordre des tomes: tome I (1834); tome II (1835); tome III (1836); tome IV (1837); tome V (1839); tome VI (1844); tome VII (les deux fascicules: 1854); tome VIII (1841); tome IX (1854). L'avertissement du dernier tome indique: "Cette dernière division de l'Erpétologie (les Urodèles) était rédigée, dès l'année 1841, lorsqu'à paru le VIII ème volume qui commençait l'histoire du quatrième ordre, celui des Batraciens ...".

C'est donc le fascicule 2 du tome VII qui, en réalité, a été le dernier écrit. A cette époque (1854) Bibron n'existait plus, il était mort en 1848, Constant Duméril et son fils ont du vouloir mettre un terme à leur publication et ont rapidement rédigé certains chapitres comme le chapitre VII qui contient les *Elaps*. Là, ne figurent plus les mensurations si fréquentes dans les autres chapitres, ni les comptes de ventrales et de sous-caudales. On peut s'étonner de ces trop brèves descriptions. Il se peut que les Duméril qui avaient à ce moment là des relations constantes avec le Professeur Jan, Directeur du Musée de Milan, aient songé à "passer la main" comme le laisse entendre la lettre d'Auguste Duméril (1858) qui figure au début du "Plan d'une Iconographie descriptive..." de Jan (1858, *Rev. Mag. Zool.*, sér. 2, 10:438-449). Cela explique peut être que Jan ait commencé ce "Plan" par l'étude des *Elaps* (p. 446 et note p. 447) compétée par la suite (1858, *Rev. Mag. Zool.*, sér. 2, 10:514-527; 1859, id., sér. 2, 11:122-136 et 148-159, pl. 4, 5 et 9). Ces 3 derniers articles ont été regroupés avec des *modifications de texte* (2) plus ou moins importantes dans un tiré à part intitulé cette fois "Prodrome d'une Iconographie descriptive...", mais où les planches 4, 5 et 9 sont indiquées comme 4, 5 et 6 et où cinq planches A, B, C, D, E ont été ajoutées (2 en couleurs concernant les *Micrurus* et 3 en noir pour d'autres Elapidés et quelques Hydrophiidés).

Après le "Plan..." et le "Prodrome" Jan a fait de nouvelles corrections intitulées "Additions et rectifications..." (1859, *Rev. Mag. Zool.*, sér. 2, 11:505-512).

Tous ces travaux de Jan sont d'une importance notable pour l'étude des *Micrurus* de nos collections.

- (1) A ce propos, je dois signaler, que le n.° de collection est celui qui figure sur le parchemin attaché en permanence au corps de l'animal. Il correspond au même numéro des registres d'entrées de collection. Comme on peut le constater plus loin, K. P. Schmidt, lors de son passage à Paris en 1932, a uniquement relevé le numéro de rangement du bocal renfermant le ou les animaux et non le numéro d'entrée. De plus il a mal calligraphié ces numéros. Cels a provoqué une certaine confusion et je me suis efforcée de rétablir les choses dans ce travail.
- (2) H. M. Smith, en 1943, dans les *Transactions Kansas Academy Science*, 46:241-242, a essayé de donner les correspondences de pagination entre le "Plan" et le "Prodrome" sans toutefois donner le détail des différences des textes des deux publications.

Genre *MICRURUS* Wagler, 1824.

Wagler, 1824, Serp. Brasil. spec. : 48.

Espèce-type *Micrurus spixii* Wagler, 1824.

Elaps gastrodelus Duméril, Bibron et Duméril, 1854, Erp. Gén., VII:1212.

Holotype : MNHP 3930 : localité inconnue.

Keraudren (1).

Spécimen en alcool, très bon état : ♂.

LT:340 mm; Q:21 mm.

V:228; A/2; SC:22/2.

Anneau clair derrière les pariétales suivi par 41 demi-anneaux clairs ventraux, dessous de la queue clair.

Schmidt (1937) suppose que le type de Duméril, Bibron et Duméril est le n.º 4626 c du Muséum National de Paris. C'est inexact, puisque ce dernier spécimen (en réalité portant le n.º MNHP 1898 — 5) a été récolté par Mme Hyver en Guyane en 1898. L'holotype est bien le n.º 3930, spécimen examiné en 1913 par J. C. Thompson qui a remarqué que cet individu comporte 1 + 1 temporales sur le côté droit de la tête et 0 + 1 temporale sur le côté gauche, ce que je peux confirmer ici.

Ce spécimen est aussi cité par Hoge et Romano (1965) et par Brongersma qui, en 1966, a fait le point de l'historique d'*Elaps collaris* et en même temps de celui d'*Elaps gastrodelus*.

= *Micrurus collaris* (Schlegel, 1837)

Elaps bocourti Jan et Sordelli, 1872, Icon. Gén. Ophid., liv. 42, pl. 6, f. 2.

Holotype: MHNP 869: Localité inconnue (restreinte par Roze (1967) à Rio Daule, province de Guayas (Equateur).

Liautaud (1843).

Spécimen en alcool, très bon état: ♂.

LT: 283 mm; Q: 39 mm.

V: 194; A/2; SC: 49/2.

Dessus de la tête noir. Anneaux noirs en 18 triades sur le corps + 7 larges anneaux noirs sur la queue.

Ce spécimen est représenté en grandeur nature sur la planche de Jan et Sordelli. C'est aussi un des syntypes de *Elaps circinalis* Duméril, et Bibron et Duméril, 1854.

(1) on sait seulement que Keraudren, médecin de la Marine, a envoyé des collections des Antilles et d'Amérique du Sud.

= *Micrurus bocourti bocourti* (Jan et Sordelli, 1872).

Elaps diastema Duméril, Bibron et Duméril, 1854, *Erp. Gén.* VII: 1222.

Il y avait à l'époque des Duméril, 3 syntypes provenant du Mexique: 2 spécimens récoltés en 1847, sans indication de donateur et un troisième, récolté par Ducommun (entré en collection en 1838, d'après nos catalogues), jugé en très bon état par les descripteurs.

Schmidt, lors de son passage à Paris, en 1933, a négligé ce dernier spécimen qui était le seul syntype existant alors dans nos collections. Il a choisi comme lectotype un autre individu du Mexique donné par Schlumberger en septembre 1859 (ancien n° de rangement 4620; en réalité n° MNHP 7656). Ce spécimen, à queue tronquée, était donc entré en collection quelques années après la parution de l'*Erpétologie Générale*. Il n'y a donc aucune raison d'accepter le choix de Schmidt.

Seul, à l'heure actuelle, le n° 7657 peut être considéré comme le lectotype d'*Elaps diastema* puisqu'étant le seul syntype, de Duméril, Bibron et Duméril, encore dans nos collections.

Lecto type: MNHP 7657: Mexique.
Ducommun (1838).

Spécimen en alcool, très bon état: ♀.

LT: 607 mm; Q: 69 mm.

V: 213; A/2; Q: 1/2 + 4 + 35/2.

Anneaux noirs: 1 nuchal + 15 complets + incomplet sur le corps + 4 sur la queue (soit les 21 anneaux indiqués par Dum., Bib. et Dum.).

= *Micrurus diastema* (Duméril, Bibron et Duméril, 1854).

Elaps epistema Duméril, Bibron et Duméril, 1854, *Erp. Gén.* VII: 1222.

Holotype: MHNP 3922: Mexique
Verreaux.

Spécimen en alcool, très bon état: ♂.

LT: 612 mm; Q: 83 mm.

V: 195; A/2; V: 45/2.

Un anneau noir nuchal + 10 taches noires dorsales + 4 anneaux sur la queue.



+ *Micrurus diadema* (Duméril, Bibron et Duméril, 1854)

Elaps apiatus Jan, 1858, *Rev. Mag. Zool.*, (2), 10:522, pl. A.

Holotype: MHNP 3920: Vera Paz (Guatemala).
Morelet (1849).

Arthur Morelet a rapporté des Reptiles du Vera Paz en 1849 (Erp. Gén. VII, pp. 211, 1146 ...). Jan avait écrit "Vera Cruz, ce qui est un lapsus; ceci avait été déjà corrigé par K. P. Schmidt en 1933.

Spécimen en alcool, à queue légèrement amputée, un Caecilidae était avalé en partie par le spécimen qui est assez bon état: ♂.

LT: 400 (+) mm; Q: 45 (+) mm.

V: 204; A/2; SC: 8/1 + 30/2 (+).

Anneaux noirs: 1 nuchal + 29 sur le corps + 10 sur la queue (+).

= *Micrurus diastema* (Duméril, Bibron et Duméril, 1854)

Elaps affinis Jan, 1858, *Rev. Mag. Zool.*, (2), 10:522, pl. B et Jan et Sordelli, 1872, *Icon. Gén. Ophid.*, liv. 42, pl. 1, f. 2 (sous le nom de *Elaps fulvius affinis*).

Holotype figuré: MNHP 3921: Mexique.

Spécimen en alcool, en très bon état: ♀.

LT: 718 mm; Q: 73 mm.

V: 217; A/2; SC: 39/2.

Anneaux ou fractions d'anneaux noirs: 1 nuchal + 20 sur le corps + 6 sur la queue.

Schmidt (1933) écrit "*Micrurus affinis* was based on two specimens in the Museum d'Histoire Naturelle in Paris (n° 4624)". Schmidt donne une fois encore le n° de rangement au lieu du n° de collection. Manifestement Jan ne parle que d'un spécimen dans sa description. Le deuxième spécimen étiqueté *Elaps affinis* au moment du passage de Schmidt (MNHP 1153) n'est entré dans nos collections qu'en 1863, date postérieure à celle de la description de Jan.

La figure de la planche B du travail de Jan représente l'holotype (MHNP 3921); c'est aussi ce spécimen qui est figuré sur la planche de l'Iconographie avec tous ses détails de coloration que nous observons encore à l'heure actuelle.

Il reste toutefois un petit problème difficile à résoudre. L'écaillure donnée par Jan correspond bien à ce que j'ai pu relever; en revanche les mensurations ne correspondent pas: s'agit-il d'erreurs typographiques comme on en trouve quelques unes dans les travaux de Jan ou erreur de transcription de sa part? Il est difficile de trancher.

= *Micrurus diastema* (Duméril, Bibron et Duméril, 1854)

Micrurus affinis stantoni Schmidt, 1933, *Field Mus. Nat. Hist. Chicago, Zool. Ser.*, XX, :36.

Schmidt a choisi deux de ses paratypes dans nos collections n° 4614 et 4614 J. Une fois encore ce sont les anciens n° de rangement. Ils correspondent aux n° de collection 3917 (4614) et 1898-253 (4614 J).

Je les ai examinés successivement.:

Paratype MNHP 3917; Mexique.

Spécimen an alcool, état moyen.

LT: 389 mm; Q: 54 mm.

V: 195; A/2; SC: 49/2.

Anneaux noirs: 1 nuchal + 15 sur le corps + 6 sur la queue.

J'ai suivi la synonymie de cette sous-espèce dans la littérature: 1933, Schmidt = *Micrurus affinis stantoni*, 1936, Schmidt = *Micrurus affinis alienus*, 1967, Roze = *Micrurus diastema sapperi*, lequel est suivi par Peters et Orejas-Miranda en 1970, puis par Hoge et Romano en 1971, pour aboutir en 1973, chez Frazer à *Micrurus diastema*. Ce que je puis confirmer.

= *Micrurus diastema* (Duméril, Bibron et Duméril, 1854)

Dans l'ignorance des cheminements antérieurs qui avaient conduit ce spécimen à être encore catalogué, à tort, à l'époque de Schmidt comme *Elaps fulvius* (1), je me demande si, ce spécimen ne serait pas à l'origine un des syntypes manquants d'*Elaps diastema* Dum., Bib. et Dum. Je le soupçonne, mais je ne peux le prouver.

Quant au deuxième syntype manquant, ne pourrait-on pas cette fois supposer que le spécimen du Mexique, envoyé par A. Duméril à Jan au moment de l'Iconographie, et décrit ensuite par Jan sous le nom d'*Elaps affinis* (2) n'était pas lui aussi primitivement étiqueté *Elaps diastema*. Cette éventualité me paraît probable. Et cela prouverait que Duméril, Bibron et Duméril avaient vu juste à leur époque en groupant les spécimens 7657 (*diastema*), 3921 (*affinis*), 3917 (*affinis stantoni*) sous un seul vocable. Ce qui se trouve maintenant parfaitement justifié à la lecture du travail de Frazer (1973) c'est à dire 120 ans plus tard.

Le cas du deuxième paratype de *M. affinis stantoni* de Schmidt est lui aussi complexe:

- (1) Ici, comme on le verra plus bas, A. Duméril, responsable des collections jusqu'en 1870 avait suivi, son catalogue méthodique de nos archives en fait foi, la classification de l'Elenco de Jan qui classe *diastema* parmi les varétés d'*Elaps fulvius*.
- (2) Je ferai remarquer que Jan dans son Elenco, fait, d'*Elaps affinis*, comme de *diastema* une variété d'*Elaps fulvius*.

Paratype MHNP 1898-253: Cerro San Juan, versant occidental, territoire de Tepic (Mexique Ouest, Nayarit)

Diguet.

Spécimen en alcool, bon état: ♀.

LT: 597 mm; Q: 61 mm.

V: 221; A/2; SC: 42/2; temp.: 1 + 2.

Anneaux noirs: 1 nuchal + 24 sur le corps + 7 sur la queue.

Ce spécimen avait été déterminé à son arrivée par Mocquard, comme *Elaps fulvius* (*Bull. Soc. Philom. Paris*, 1899, 9, I:157). Smith et Taylor en 1945 (*Bull. U. S. Nat. Mus.* 187:173, note 186 font de ce spécimen un *Micrurus diastema distans* (Kennicott), espèce séparée de *diastema* par Zweifel (1959) et Roze (1967) et nous arrivons à *Micrurus distans distans*; ce qui paraît tout à fait justifié pour ce spécimen

= *Micrurus distans distans* (Kennicott, 1860)

Elaps dumerilii Jan, 1858, *Rev. Mag. Zool.*, (2), 10:522, pl. A; Jan et Sordelli, 1872, *Icon. Gén. Ophid.*, liv. 42, pl. I, f. 3.

Holotype figuré: MNHP 3923: Carthagène (Colombie)
Barrot.

Spécimen en alcool: très bon état: ♂.

LT: 660 mm; Q: 100 mm.

V: 202 (1); A/2; SC: 51/2.

Anneaux noirs: 1 nuchal + 11 triades sur le corps + 6 anneaux sur la queue.

Ce spécimen avait été d'abord décrit par Duméril, Bibron et Duméril dans l'Erpétologie Générale (VII: 1211) sous le nom de *Elaps Margrivi*. C'est d'ailleurs ce qu'écrivit Jan dans "Additions et rectifications aux plan et prodrome de l'Iconographie descriptive des Ophidiens (1859, *Rev. Mag. Zool.*, (2), 11:509).

C'est aussi ce spécimen qui figure sur la planche de l'Iconographie.

= *Micrurus dumerilii dumerilii* (Jan, 1858)

Micrurus elegans veraepacis Schmidt, 1933, *Field Mus Nat. Hist., Zool. Ser.*, 20:32.

Paratype: MNHP 1262: Haute Vera Paz, région autour du Rio Coban, Cap Coban (Guatemala).

Bocourt (Commission scientifique du Mexique)
1868.

(1) Jan donne, par erreur: 104.

Spécimen en alcool, très bon état: ♀.

LT: 485 mm; Q: 45 mm.

V: 223; A/2; SC: 35/2.

Anneaux noirs en triades: 1/2 triade nuchale + 15 triades 1/2 sur le corps + 1/2, 2 sur la queue.

Elaps frontalis Duméril, Bibron et Duméril, 1854, *Erp. Gén.*, VII: 1223.

Des trois syntypes signalés dans l'Erpétologie Générale, nos collections ne possèdent plus que deux individus:

Syntype MNHP 854: Brésil
Claussen (1844).

Syntype MNHP 578: Côte Ferme (Vénézuéla)
Beauperthuis.

Les deux spécimens en alcool, en très bon état: ♂.

Le premier, MNHP 854, dont voici les caractéristiques:

LT: 501 mm; Q: 31 mm.

V: 235; A/2; SC: 25/2.

Anneaux en 11 triades sur le corps + 1 sur la queue.

l'anneau médian de la triade est nettement plus large que les deux qui l'entourent, à la fois dorsalement et ventralement. Sur les côtés, il apparait comme étant de même largeur que les deux autres.

= *Micrurus frontalis frontalis* (Duméril, Bibron et Duméril, 1854)

Le deuxième, MNHP 578:

LT: 727 mm; Q: 57 mm.

V: 208; A/2; SC: 28/2.

Anneaux en 10 triades sur le corps + 1 sur la queue.

Ce syntype a été examiné en 1978 par le Professeur Hoge qui l'a déterminé:

= *Micrurus isozonus* (Cope, 1880)

Elaps heterochilus Mocquard, 1887, *Bull. Soc. Philom. Paris*, (7), 11:39.

Holotype: MNHP: 1887 — 122: Brésil
Pougnat

Spécimen en alcool, très bon état: ♂.

LT: 553 mm; Q: 43 mm.

V: 209; A/1; SC: 2/2 + 6 + 21/2.

Anneaux en triades: 12 sur le corps + 1 sur la queue.

= ? *Micrurus frontalis altirostris* (Cope, 1859).

Cette synonymie, adoptée par Roze (1967) n'est pas très satisfaisante; il est dommage de ne pas connaître le lieu exact où a été trouvé ce spécimen. Hoge et Romano (1971) écrivent: "The type specimens of *M. heterochilus* and *M. lemniscatus multicolor* are obviously intergrades."

Micrurus latifasciatus Schmidt, 1933, *Field Mus. Nat. Hist., Zool. Ser.*, 20:35.

Paratypes, MNHP 1301 et 1301 A: San Agustín, près de Solola (Guatemala.).

Bocourt (Commission scientifique du Mexique).

Spécimens en alcool, en très bon état: ♂.

Ces deux spécimens ont été choisis par Schmidt (1933, p. 35) sous les anciens numéros de rangement 4614 a (et non 4614 d comme l'écrit Schmidt).

Ces deux individus avaient été déterminés en 1896 par Dugès comme des *Elaps michoacanensis* (*Bull. Mus. Nat. Hist. nat., Paris*, 1896, II, p. 61.).

Paratype MNHP 1361:

LT: 490 mm; Q: 78 mm.

V: 189; A/2; SC: 53/2.

Anneaux noirs: 1 nuchal; + 6 sur le corps + 3 sur la queue.

Paratype MNHP 1361 A:

LT: 220 mm; Q: 33 mm.

V: 190; A/2; SC: 53/2.

Anneaux noirs: 1 nuchal + 6 sur le corps + 3 sur la queue.

Elaps mipartitus Duméril, Bibron et Duméril, *Erp. Gén.*, VII: 1220.

Holotype MNHP 3915: Rio Sucio ou Senio (= ? Sinù pour Roze, 1967)

(Nouvelle — Grenade = Colombie)

Goudot.

"... nous n'en avons que la peau très bien préparée et conservée dans l'alcool..." (Duméril, Bibron et Duméril: 1221)

LT: 762 mm; Q: 38 mm.

V: 281; A/2; SC: 23/2.

Museau noir + 64 anneaux sur le corps + 3 sur la queue.



= *Micrurus mipartitus mipartitus* (Duméril, Bibron et Duméril, 1854).

Elaps decussatus Duméril, Bibron et Duméril, 1854, *Erp. Gén.*, VII, 1221.

"Nous en possédons trois exemplaires, dont un entier et deux autres, ... Nous n'avons de ces derniers que les peaux fort bien préparées." (p. 1222).

Donc 3 syntypes, tous trois en alcool, le spécimen entier, comme les 2 peaux en bon état.

Syntypes MNHP 3916 en peau; MNHP 3916 A, entier;

MNHP 3916 B, en peau:
Nouvelle Grenade (= Colombie).
Goudot.

MNHP 3916: LT: 822 mm; Q: 48 mm.
V: 279; A/2; SC: 26/2.
Museau noir + 62 anneaux noirs sur le corps + 3 sur la queue.

MNHP 3916 A: LT: 480 mm; Q: 27 mm.
V: 298; A/2; SC: 28/2.
Museau noir + 72 anneaux sur le corps + 3 sur la queue.

MNHP 3916 B: LT 638 mm; Q: 40 mm.
V: 286; A/2; SC: 26/2.
Museau noir + 51 anneaux sur le corps + 2 sur la queue.

= *Micrurus mipartitus decussatus* (Duméril, Bibron et Duméril, 1854).

Micrurus nuchalis Schmidt, 1933, *Field Mus. Nat. Hist., Zool. Ser.* XX:35.

Schmidt a désigné 3 paratypes dans notre Musée: sous l'ancien numéro de rangement 4622 a, le MNHP 3260; sous l'ancien numéro 4619 a (écrit par erreur dans son texte 4612 a), les MNHP 4424 et 4424 A.

Paratype MNHP 3260: Mexique
Boucard

Spécimen en alcool, en bon état: ♀.

LT: 715 mm; Q: 77 mm.

V: 207; A/2; SC: 38/2.

Anneaux noirs: 1 nuchal + 7 sur le corps + 2 sur la queue (l'anneau nuchal est de 10 écailles).

Paratype MNHP 4424: Santa Efigenia, Oaxaca (Mexique).
Sumichrast par Bocourt (1875).

Spécimen en alcool, en bon état: ♀.

LT: 605 mm; Q: 68 mm.

V: 202; A/2; SC: 37/2.

Anneaux noirs: 1 nuchal (10 écailles) + 7 sur le corps + 2 sur la queue.

Paratype MNHP 4424 A: même provenance que le précédent.

Spécimen en alcool, en bon état: ♀.

LT: 578 mm; Q: 69 mm.

V: 205; A/2; SC: 38/2.

Anneaux noir: 1 nuchal (10 écailles) + 8 sur le corps + 2 sur la queue.

Elaps circinalis Duméril, Bibron et Duméril, 1854, *Erp. Gén.*, VII: 1210.

A l'origine, écrivent les auteurs, il y avait 4 syntypes: "... un seul, qui provient de M. Plée, porte pour étiquette, avec un point de doute, qu'il est de la Martinique; un autre, qu'il a été donné par M. Geoffroy, avec le nom de *corallinus*. Un troisième est un don de M. Liautaud, qui voyageait à bord de la Danaïde en 1843; et un dernier a été acquis en octobre 1846, de M. Deyrolle".

Le premier syntype a été donné par le Professeur Guibé au Professeur Hoge en 1956 (MNHP 3913); Le deuxième est encore dans nos collections (MNHP 3912); le troisième a été représenté sous le nom d'*Elaps bocourti* par Jan et Sordelli en 1872 dans l'Iconographie Générale des Ophidiens (MNHP 869) et le quatrième ne figure plus dans nos collections.

Syntype MNHP 3912: localité inconnue
Geoffroy

Spécimen en alcool, très bon état: ♀.

LT: 280 mm; Q: 25 mm.

V: 202; A/2; SC: 32/2.

Anneaux noirs: 1 nuchal + 26 sur le corps + 6 sur la queue.

= *Micrurus psyches circinalis* (Duméril, Bibron et Duméril, 1854).

Micrurus spixii martiusi Schmidt, 1953, *Fiedliana Zool.*, 34:175, f. 33-34.

Paratype MNHP 5357: Ilha do Marajo.
Jobert (1879).

Schmidt a écrit, par erreur, 5337 au lieu de 5357 (p. 172). La même erreur a été commise (p. 171): 5336 au lieu de 5356, pour un autre

paratype qui n'existe plus dans nos collections et provenant de Para. Je pense que ce dernier a été donné en 1956 au Professeur Hoge.

Spécimen en alcool, en assez bon état: ♂.

LT: 1076 mm; Q: 60 mm.

V: 207; A/2; SC: 20/2.

Anneaux noirs en triades: 7 sur le corps + 1 sur la queue.

Elaps surinamensis Cuvier, 1817, Règne animal, édit. 1, 2:84.

Syntypes MNHP 3926 et MNHP 3925: Surinam
Levaillant

C'est Duméril, Bibron et Duméril qui affirment qu'il s'agit là des deux spécimens types de Cuvier: "Ils ont été probablement été étiquetés par G. Cuvier..." (Erp. Gén, VII: 1225). Ces auteurs ont même écrit auparavant: "... le second beaucoup plus petit, provenant du Surinam, semble être le même qui aurait servi de modèle à celui qui est représenté sur la planche 6 du second volume du Trésor de Séba (fig. 2), portant pour origine le nom de Surinam".

Schmidt (1952, p. 26) donne encore une fois les n° de rangement en lieu et place des n° de collection.

Syntype MNHP 3926: Spécimen en bon état: ♂

LT: 862 mm; Q: 114 mm.

V: 169; A/2; SC: 37/2.

Anneaux noirs: 6 1/2 sur le corps + 1/2 1 sur la queue.

Syntype MNHP 3925: Spécimen en bon état: ♀

LT: 302 mm; Q: 32 mm.

V: 176; A/2; SC: 32/2.

Anneaux noirs: 8 1/3 sur le corps + 2/3 1 sur la queue.

Cette espèce se sépare immédiatement des autres *Micrurus* par ses labiales: la 4ème labiale *seule* est en contact avec l'oeil; caractère que Boulenger avait déjà signalé dans son catalogue (1896), oublié des systématiciens dans leurs tableaux de détermination et repris par Duellman tout récemment (1978).

Je dois signaler, en outre, que le n° MNHP 3924 de Cayenne récolté par Daniele (Spécimen non-type) est représenté dans l'Iconographie de Jan et Sordelli (liv. 42, pl. 3, fig. 1).

= *Micrurus surinamensis surinamensis* (Cuvier, 1817)

Remarques sur quelques spécimens non-types des Collections du Muséum national d'Histoire Naturelle de Paris et énumérés dans l'"Erpétologie Générale" de Duméril, Bibron et Duméril (1854, VII).

Page 1207:

Elaps corallinus

Le Muséum possède encore 3 spécimens vus par Dum. B. et D.

MNHP 3911: Brésil — Langsdorff

= *Micrurus corallinus* (Merrem, 1820)

MNHP 3909: Trinité — Plée

= *Micrurus psyches circinalis* (Dum., Bibr. et Dum., 1854)

MNHP 3910: Nouvelle Grenade (Colombie) Riefer.

= *Micrurus dumerili carinicauda* Schmidt, 1936

Page 1211:

Elaps alternans

Cette espèce insuffisamment décrite dans l'Erp. Gén., ne se retrouve plus ultérieurement dans la littérature. Boulenger lui-même la laisse de côté et n'en parle pas.

Duméril, Bibron et Duméril ont vu deux spécimens, provenant du Mexique et rapportés par Prémat en 1843. J'ai retrouvé trace de 3 *Elaps* sp. sur un vieux catalogue, effectivement récoltés au Mexique par Prémat. Les deux individus ayant servi pour la description d'*E. alternans* n'existent plus dans nos collections. Seul le MNHP 3919 (qui est un *Micrurus diastema*) est étiqueté Mexique — Prémat. Il ne correspond donc pas à la description d'*Elaps alternans*.

Page 1212:

Elaps psyches

Duméril, Bibron et Duméril mettent dans leur synonymie: "1803. *Vipera Psyche*. Daudin. Rept. 8, p. 320, pl. 100, fig. 1" et dans leur description:

"Le Musée de Paris possède trois exemplaires de ce Serpent. L'un d'eux qui a servi à la description que Daudin en a faite, provient du Surinam; il a été rapporté par Levaillant, et a passé ensuite dans la collection de Dufresne; un autre a été rapporté de la Guyane par M. Leschenault, et le troisième de Cayenne, par Claude Richard..."

Nous possédons bien dans nos collections 3 spécimens contemporains des Duméril:

MNHP 7654: Surinam — Levailant.

MNHP 8669: Guyane — Leschenault.

MNHP 3914: Cayenne — Richard.

Les n° 8669 et 3914 ne posent aucun problème. Seul le n° 7654, indiqué par Dum., Bib. et Dum., comme le type de Daudin amène quelques remarques.

On lit dans Daudin (1803, *Hist. Rept.* 8:320) en note en bas de page:

“(1) *Vipera psyches; annulis alternatim fuscis et atris circa 56 circulo albo separatis; caudâ acutâ 1/9. Scutis abdom. 188. — Scutellis subcaud. 45-233.*”

Apparemment, au vu du nombre des écailles abdominales, 188 et des sous-caudales, 45, on peut en déduire qu'il s'agit d'un spécimen ♂.

Dans son texte de la p. 320, Daudin indique que son spécimen mesure 9 pouces soit 244 mm (1 pouce français = 27,07 mm). Ensuite p. 321 “... le reste de l'animal est très agréablement orné de 56 anneaux ou environ...”

Or le MNHP 7654 mesure 490 mm de longueur totale (dont 48 mm de queue) soit presque le double du spécimen de Daudin. J'ai compté 203 ventrales et 30/2 sous-caudales et le nombre total d'anneaux (rouges + noirs) est de 80 environ. Je ne suis pas sûre de ce nombre qui est difficile à évaluer, l'animal étant desséché et en mauvais état.

Donc, étant donné la taille et les nombres d'écailles de ce spécimen; il m'est impossible, malgré sa provenance, d'affirmer que nous sommes en présence du type de Daudin. Ce qui est évidemment regrettable.
Page 1215:

Elaps fulvius

Du très “... grand nombre d'exemplaires ...” cités par Duméril; Bibron et Duméril, restent en collection seulement 3 spécimens:

MNHP 888: Savannah — Harpert.

MNHP 59: Nouvelle Orléans — Barabino.

MNHP 3918: Nouvelle Orléans — Fournier.

Page 1217:

Elaps lemniscatus

Sur les “... 20 exemplaires de toutes dimensions...” nous retrouvons les n°:

MNHP 3928: Bahia — Dabadie.

MNHP 7659: Bahia — Dubois.

MNHP 7658: Cayenne — Mélinon.



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SERPIENTES DE VENEZUELA

DISTRIBUCIÓN GEOGRAFICA Y ALTITUDINAL DE GENEROS DE SERPIENTES EN VENEZUELA

Abdem Ramon LANCINI V. *

Venezuela está ubicada en el extremo norte de América del Sur y tiene una superficie de 912.050 kilómetros cuadrados y recientemente incorporó a su territorio 4.395 kilómetros cuadrados adicionales, en un acuerdo bilateral en la revisión de límites con la República Federativa del Brasil.

La posición geográfica del país está ubicada en sentido latitudinal entre 0° 45' 0" y 12° 11' 46" Norte y entre 59° 45' 79" hasta 73° 11' 49" de longitud Oeste.

Todo el Norte del país está bañado por una costa de 2813 Kms. y tiene una frontera meridional con el Brasil de 2.000 kilómetros de extensión. Sus límites con Colombia son de 2.050 kilómetros y de 743 con Guyana.

Como puede observarse, en lo referente a latitud, Venezuela es un país ecuatorial y predominan en gran parte de su territorio los climas tipo "A" (cálidos y húmedos), "B" (secos) y en menor proporción los del tipo "G" y "H" (tempestades tropicales y fríos de alta montaña tropical); según la clasificación de Köppen.

Las distancias extremas del territorio venezolano son de 1271 kilómetros de Norte a Sur y 1.493 kilómetros de Este a Oeste.

Desde el punto de vista altitudinal, el relieve del país se extiende desde el nivel del mar hasta 5.007 metros de altura en el pico Bolívar de los Andes de Mérida. Es fácil comprender que el factor vertical es el más importante en la distribución de la temperatura media en las regiones naturales de Venezuela. Por otra parte, la posición ecuatorial intertropical del país y la gran variedad de pisos térmicos altitudinales existentes, ha permitido la existencia de ambientes desérticos como las dunas del Istmo de los Médanos y península de la Guajira, hasta los páramos con nieves perpetuas por encima de 4.700-4.850 metros de altitud.

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La vegetación del país, muy rica en variedad de formaciones (selvas, sabanas, dunas y páramos), abriga un número significativo de géneros, especies y subespecies de Serpientes recientes. Actualmente se conocen alrededor de 150 especies y subespecies, agrupadas en siete (7) Familias y cincuenta y dos (52) géneros. El 20% de la Ofiofauna de Venezuela comprende a Serpientes venenosas de las familias *Elapidae* y *Viperidae* y otro 20% lo forman especies semivenenosas de la familia *Colubridae*. El restante 60% corresponde a especies y subespecies no venenosas de varias Familias. No obstante, estos porcentajes pueden variar en el futuro con nuevos descubrimientos herpetológicos.

Las costas de Venezuela e islas adyacentes, al igual que todo el Norte del país están sometidos a la influencia de los vientos Alisios del Nordeste, que determinan una estación seca de cinco meses y otra lluviosa de siete meses. En cambio, al Sur del río Orinoco la estación lluviosa es más prolongada.

En las costas de Venezuela la vegetación generalmente es semi-xerófila e a veces desértica y así como hay pobreza de vegetación, los elementos faunísticos son poco numerosos en especies.

Aproximadamente el 18% de las especies de Serpientes del país se encuentran en esta extensa y estrecha región (incluyendo islas de Venezuela en el mar Caribe) considerada en su totalidad.

En las zonas muy áridas de las Penínsulas de Araya, Paraguaná y la Guajira la vegetación es muy pobre, las temperaturas con una variación diurna-nocturna muy amplia y la humedad relativa del aire muy baja. En ese medio hemos encontrado especies de 14 géneros: *Leptodeira*, *Leptophis*, *Masticophis*, *Mastigodryas*, *Oxybelis*, *Phimophis*, *Pseudoboa*, *Spilotes*, *Tantilla* y *Thamnodynastes* de la familia *Colubridae*. *Leptotyphlops* (*Leptotyphlopidae*), *Thyphlops* (*Typhlopidae*) y entre las venenosas algunas pocas especies de los géneros *Bothrops*, *Crotalus* (*Viperidae*) y *Micrurus* (*Elapidae*).

En contraste con las regiones bajas xerófilas (-100 m.) de las costas y algunas otras porciones del interior del país, encontramos los sistemas montañosos de los Andes y Perijá en el Occidente y la Cordillera de la Costa en el Norte y Este de la Nación.

En los Andes de Táchira existe una región de particular interés, la región del Páramo de Tamá, limítrofe con Colombia. Allí existen elevaciones de poco más de 3.600 metros de altitud y se han encontrado formas endémicas de plantas y animales. Hasta el presente hemos hallado allí 7 géneros de serpientes, entre ellos *Lampropeltis* (*Colubridae*), extendido desde Canadá hasta Ecuador.

Entre la región del páramo de Tamá (3.329 m.) y los Andes de Mérida hay una depresión de origen tectónico, denominada Depresión del Táchira, con un desnivel de más de 2.000 metros para luego elevarse nuevamente. Esto ha constituido una interesante barrera ecológica para muchas especies propias de la Cordillera Oriental de los Andes de Colombia, que no penetran hacia los Andes de Mérida y la cuenca hidrográfica del Lago de Maracaibo.

La Sierra Nevada de Mérida es la formación orográfica más alta de Venezuela. Ella se extiende paralelamente a la depresión suroriental del Lago de Maracaibo (-10 a - 100 m.) y exhibe todos los pisos térmicos altitudinales existentes en el país, desde casi el nivel del mar a orillas del Lago de Maracaibo, hasta 5.007 metros. Debemos recordar que la temperatura media al nivel del mar en Venezuela es de 27°C y va disminuyendo progressivamente con la altura. Así, por ejemplo, a 1.000 metros la temperatura media anual es de +21°C; a 2.000 metros +15°C; a 3.000 metros +9°C; a 4.000 metros +2°C y, por último, a 5.000 metros -5°C.

La mayoría de los géneros y especies de Serpientes se encuentran en los pisos macrotérmicos (0 - 100 m.) y mesotérmicos (1.000 - 2.800 m.), en ambientes con temperaturas medias anuales entre 28°C y 13,5°C. En cambio, por encima de 3.000 metros de altitud apenas se encuentran unos pocos géneros (*Atractus* y *Leimadophis*, principalmente) de la Familia *Colubridae* y, ocasionalmente, serpientes ponzoñosas *Bothrops* (*Viperidae*) y *Micrurus* (*Elapidae*). Allí, las pocas especies que habitan permanecen ocultas debajo de rocas y plantas en busca de temperaturas y porcentajes de humedad un poco más elevados que en la superficie. Por otra parte, cabe destacar que en sistemas montañosos de otros continentes a mayor altitud todavía se encuentra cierto número de géneros y especies de serpientes y de otros animales y plantas, a diferencia de los Andes Suramericanos. Esto se explica porque el clima andino presenta pronunciadas oscilaciones en el ritmo de la temperatura diurna y nocturna, sobre todo por encima de los 4.000 metros de altitud.

En los páramos andinos, después de 3.000 metros de altura apenas encontramos un 3% de la ofiofauna conocida de Venezuela. En contraste con esa dispersión vertical, apenas a unos 375 kms. en línea recta al nordeste de la Sierra Nevada de Mérida, se encuentran las dunas del Istmo de los Médanos en la Península de Paraguaná, cuyo suelo arenoso, desnudo o con vegetación escasa como en las partes más elevadas de los Andes. Allí hay microclimas inversos, con temperaturas medias muy elevadas, baja humedad relativa del aire y niveles altitudinales inferiores a los 100 metros sobre el nivel del mar. En la península de Paraguaná la duración de las horas de insolación llega a promedios de nueve (9) horas diarias y los vientos alisios soplan del nordeste a una velocidad media de 22 - 24 kilómetros por hora. En estos ambientes xerófilos extremos hemos capturado solamente el 2-3% de las especies de Serpientes de Venezuela.

Otra peculiaridad biogeográfica que ofrece la Península de Paraguaná es la existencia del Cerro Santa Ana, que emerge del centro de la península desde poca altura sobre el nivel del mar hasta más de 800 metros. Las partes altas del cerro presentan una importante vegetación boscosa y su fauna poco estudiada debe ser de gran interés científico. Desde el punto de vista climatológico el Cerro Santa Ana representa una isla climática de tipo "A" dentro de una región de clima "B".

Las Cordilleras de Perijá y de la Costa constituyen los sistemas orográficos del norte de Venezuela. La primera recorre parte de la frontera occidental colombo-venezolana y tiene elevaciones importantes de

hasta poco más de 3.000 metros de altitud. Se han hecho pocos muestreos de herpetofauna en la Sierra de Perijá, que seguramente encierra nuevas especies de Serpientes para la Ciencia o para Venezuela.

La Cordillera de la Costa es una prolongación de la Cordillera de los Andes y su herpetofauna tiene afinidades genéricas à específicas con la herpetofauna andina.

La Cordillera de la Costa tiene tres regiones delimitables: 1) Tramo Occidental, 2) Tramo Central y 3) Macizo Oriental. Este último guarda relación con la fauna de la Isla de Trinidad, Delta del Orinoco y región de las Guayanas y Amazonia. Diversos géneros de serpientes son comunes a todas estas regiones biogeográficas.

El tramo occidental de la Cordillera de la Costa presenta un relieve con alturas discretas. En cambio el Tramo Central llega a 2.765 m. en el pico Naiquatá. Igualmente en el macizo Oriental el pico Turumiquire presenta elevaciones cercanas a los 3.000 metros.

Durante muchos años hemos recolectado especies de Serpientes en el tramo central (Cordón Litoral, etc.) pertenecientes a los géneros Boa y Epicrates (Boidae), Atractus, Chironius, Clelia, Dendrophidion, Dipsas, Drymarchon, Erythrolamprus, Imantodes, Lampropeltis, Leptodeira, Leptophis, Lygophis, Mastigodryas, Ninia, Oxybelis, Oxyrhopus, Pseudoboa, Pseustes, Rhadinae, Sibon, Spilotes, Stenorrhina, Tantilla, Umbrivaga, Xenodon (Colubridae), Leptotyphlops (Leptotyphlopidae), Helmintophis (Typhlopidae), Micrurus (Elapidae), Bothrops y Crotalus (Viperidae), que hace un total de 33 géneros de los 52 conocidos del país. El número de especies encontradas en esta importante región orográfica representa aproximadamente el 30% del total.

Examinemos ahora una de las regiones naturales más extensas de Venezuela: los Llanos. Como su nombre lo indica, se trata de extensas sabanas de poca elevación (30 - 200 m.s.n.m.), que en el pasado geológico estuvieron cubiertas, en gran extensión, por un mar epicontinental. Esas llanuras se encuentran en dirección este-oeste entre los meridianos 62°-71° Oeste y entre los paralelos 7° - 10° Norte.

Se dividen en Llanos Occidentales (100 - 200 m.s.n.m.), Llanos Centrales (promedio + 100 m.s.n.m.) y Llanos Orientales, con sabanas aluvionales con niveles, en el sur de los Estados Anzoategüi y Monagas, de menos de 50 m.s.n.m. Sinembargo, hay regiones de los Llanos Orientales con mayor elevación, que reciben el nombre de Mesas.

En los Llanos de Venezuela viven por lo menos el 15% de especies de Serpientes, agrupadas en más de 30 géneros.

En los Llanos las temperaturas medias son elevadas (26° - 28°C) y la pluviosidad sobrepasa 1.100 m.m. anuales.

En el Sur de Venezuela existen también Sabanas Altas en Guayana y el Territorio Federal Amazonas. Se presentan en las laderas y cumbre de los Tepuyes en el piso mesotérmico (1.200 - 2.800 m. s.n.m.). Allí las temperaturas medias alcanzan un máximo de 22° - 24°C y la pluviosidad puede ser superior a 3.000 m.m. En las Sabanas Altas del Sur del país se encuentran varias especies interesantes de serpientes.

Una mención especial merecen las cuencas hidrográficas del Lago de Maracaibo y del río Orinoco.

El Lago de Maracaibo está situado en el occidente del país en una depresión de bajo nivel y rodeado en gran parte por selvas pluviales macrotérmicas, surcadas por numerosos ríos que desembocan en él. Allí se encuentra un número importante de géneros de Serpientes, entre ellos *Helicops*, de la familia *Colubridae*, con una especie semiacuática: *Helicops scalaris*.

La cuenca hidrográfica del Orinoco es la más importante de Venezuela, con numerosos ríos tributarios. Allí viven todos los géneros de serpientes dulce-acuícolas del país: *Eunectes*, *Helicops*, *Hydrops*, *Hydrodynastes* y *Pseudoeryx*, con un total de 7 especies y subespecies. Las serpientes de estos grupos taxonómicos son prisioneras en su distribución de esas cuencas hidrográficas con niveles desde 0 metros a 300 metros sobre el nivel del mar y climas de tipo "A".

La Amazonia de Venezuela está situada al sur del río Orinoco y constituye una prolongación de la gran Hylea amazónica del Brasil y otros países cercanos. Es la región más rica en herpetofauna de Venezuela, por su extensión y su baja posición latitudinal (0° 7.° N.). En su relieve, están presentes varios pisos térmicos, porque tiene tierras bajas (selvas y sabanas) desde + 100 m. hasta elevadas montañas tabulares, denominadas tepuyes, que alcanzan hasta 3.000 m. En la Serranía La Neblina, en la frontera Venezuela-Brasil el Pico La Neblina tiene 3.014 metros de altitud (Brasil).

El Territorio Amazonas posee tres (3) tipos principales de climas tropicales (Af, Am. y Aw) de la clasificación de Köppen, aunque en las regiones montañosas muy elevadas encontraremos verdaderas islas climáticas subtropicales. Estos tipos climáticos están estrechamente relacionados con las formaciones vegetales y la fauna que vive en ellas.

En toda la Amazonia venezolana las especies de serpientes y lagartos que allí se encuentran, están vinculadas a cuatro (4) grandes tipos de habitats, a saber:

1) Región de las selvas hidrófilas megatérmicas, que abarca gran parte de los bosques amazónicos del Territorio, especialmente en el Sur. Está bajo la influencia de un clima "Af", lluvioso todo el año, con temperaturas medias superiores a 28°C y precipitaciones anuales hasta de 3.400 a 3.600 m.m.

2) Región con predominio de sabanas. Situada principalmente en la mitad norte del Territorio, con altitudes variables (100 a 500 m.). En esta región los climas dominantes son los tropicales de sabanas (Aw.) y monzónico (Am.). Las temperaturas medias y la precipitación también son muy elevadas en esta región zoogeográfica pero hay una estación seca más o menos corta. El número de especies de serpientes es menor que en los bosques amazónicos extensos, aunque en las selvas de galería y morichales de esta región se encuentra representada casi toda la herpetofauna amazónica de Venezuela, por tratarse de estrechas bandas de clima "Af" dentro de las regiones climáticas "Am" y "Aw".

Los Reptiles de las sabanas del Territorio Amazonas están relacionados con las especies de los Llanos Centrales y Orientales del país, con numerosas especies en común.

3) Región elevada de Tepuyes. Por su formación geológica muy antigua, aislamiento geográfico más o menos completo de sus cumbres y pisos altitudinales diferentes a las selvas espesas y bajas que los rodean, las partes más altas de los tepuyes son pobres en especies e individuos de serpientes, aunque con marcada tendencia hacia los endemismos.

En los tepuyes las serpientes son todavía frecuentes en las selvas de encuesta, en cambio, predominan los lagartos en las grietas de los taludes amurallados y las cumbres rocosas de esas montañas tabulares.

Sin embargo, conviene advertir que el estudio de estas regiones es incipiente desde el punto de vista herpetológico.

Quizás en un futuro próximo, con las facilidades que ofrece el helicóptero para hacer accesible la exploración de estas formaciones orográficas, se demuestre que hay menos endemismos de los que los especialistas creen y que algunas especies propias de las selvas bajas pueden penetrar en estas regiones escarpadas.

4) Región de los grandes ríos amazónicos y sus numerosos afluentes. En los cauces y remansos de los ríos, lagunas y morichales del Territorio Amazonas viven unas seis (6) especies de serpientes dulceacuícolas, que tienen hábitos acuáticos o semiacuáticos.

Por último, debemos señalar que para el Territorio Federal Amazonas se conocen, hasta el presente 48 géneros y 74 especies y subespecies de Serpientes.

No obstante, este número se elevará sensiblemente en los próximos años con nuevos descubrimientos para la Ciencia y nuevos records para Venezuela.

La región de Guayana (Estado Bolívar) tiene características ambientales muy parecidas a las del Territorio Amazonas, pero las sabanas altas son de mayor superficie (Gran Sabana) y los tepuyes más numerosos. Estas formaciones de arenisca alcanzan en esta región su mayor altitud en el Monte Roraima (2.772 m.).

En la Guayana venezolana también se encuentra más de la mitad de las especies de Serpientes de Venezuela y muchas de ellas están dispersas en un verdadero arco zoogeográfico cuyos extremos se encuentran en la Península de Paria y la región del Alto Río Negro y el canal natural del Casiquiare.

RESUMEN

1. Venezuela es un país intertropical con un relieve desde el nivel del mar hasta 5.007 metros. El país presenta desde áreas xerófilas e incluso dunas de poca extensión, hasta regiones cubiertas por nieves perpetuas, aunque la mayor superficie la ocupan bosques y sabanas.



2. Actualmente se conocen en Venezuela alrededor de 150 especies y subespecies de Serpientes, agrupadas en 7 familias y 52 géneros.
3. Uno de los géneros más interesantes de Serpientes de Venezuela es *Atractus* de la familia *Colubridae*. En el país se conocen 16 especies de este género, sin ninguna subespecie. *Atractus* tiene una distribución altitudinal conocida desde +200 m. (*Atractus trilineatus*) hasta 3.000 metros de altitud.
4. En las costas de Venezuela (2.813 km) y tierras bajas adyacentes, consideradas en su conjunto, encontramos el 18% de la ofiofauna. Además, Venezuela posee una serie de islas de origen continental con una herpetofauna estrechamente relacionada con la de tierra firme.
En las pequeñas áreas desérticas de las costas solo hay un 2% a 3% de especies, aumentando este número al 15% en los Llanos, sabanas altas, etc. Otro 3% habita en la faja de 2.800-3.200 metros en los Andes y alrededor de un 20% a 25% en los pisos macro-térmico y mesotérmico de los sistemas montañosos de la Costa y los Andes.
Estos porcentajes aumentan a casi el 50% de las especies y subespecies en las regiones al sur del Orinoco. Además, de los 52 géneros de Serpientes hallados por ahora en el país, 48 se encuentran por debajo de 6° de latitud norte.
5. Los tipos climáticos predominantes en Venezuela son: A, B y G, con variados subtipos (Clasificación de Köppen). En lista anexa se mencionan los géneros de Serpientes de Venezuela, niveles altitudinales donde ocurren y tipo de clima de su distribución. Puede observarse cómo algunos géneros de Serpientes habitan en más de un piso térmico y soportan la influencia de más de un tipo climático. Otros géneros presentan limitaciones ecológicas.
6. La mayoría de los géneros de Serpientes de Venezuela son propios de América Tropical y unos pocos tienen una distribución geográfica más extensa.
7. La distribución altitudinal es pobre en representación genérica y específica por encima de la faja de 3.000 metros de altitud, a diferencia de sistemas orográficos de otros continentes.
8. El género *Umbrivaga* (Colubridae) es el único hasta ahora endémico de Venezuela. También se conocen algunas especies de serpientes endémicas del país.
9. El 60% de las Serpientes conocidas hasta el presente (1981) de Venezuela, no son venenosas.
10. Las Serpientes venenosas de Venezuela representan el 20% de las conocidas hasta el presente (1981) en el país. Otro restante 20% lo forman especies y subespecies de Serpientes semi-ponzoñosas opistoglifas (Colubridae).

LISTA DE GENEROS DE SERPIENTES DE VENEZUELA (1981)

<i>Generos</i>	<i>Distribucion por Tipo Climatico (KÖPPEN)</i>	<i>Niveles Altitudinales</i>
<i>ANILIIDAE</i>		
Anilius	A	30 — 700m.
<i>BOIDAE</i>		
Boa	A, B	0 — 1.500m.
Corallus	A, B	0 — 1.000m.
Epicrates	A, B	0 — 1.300m.
Eunectes	A	0 — 850m.
<i>COLUBRIDAE</i>		
Atractus	A, G	200 — 3.100m.
Chironius	A, G	0 — 2.500m.
Clelia	A	50 — 1.800m.
Dendrophidion	A, G	400 — 1.600m.
Dipsas	A, G	0 — 2.200m.
Drymarchon	A, B	0 — 2.100m.
Drymobius	A	200 — 1.400m.
Drymoluber	A	100 — 800m.
Erythrolamprus	A, G	0 — 1.800m.
Helicops	A	0 — 500m.
Hydrodynastes	A	0 — 500m.
Hydrops	A	0 — 300m.
Imantodes	A, G	0 — 1.500m.
Lampropeltis	A, G	100 — 2.600m.
Leimadophis	A, G	0 — 3.200m.
Leptodeira	A, B, G	0 — 1.600m.
Leptophis	A, B, G	0 — 1.200m.
Liophis	A, G	100 — 2.000m.
Lygophis	A	0 — 1.200m.
Masticophis	B	0 — 1.000m.
Mastigodryas	A, B, G	0 — 1.800m.
Ninia	A, G	0 — 2.000m.
Oxybelis	A, B	0 — 1.800m.
Oxyrhopus	A, G	0 — 1.700m.
Philodryas	A	0 — 500m.
Phimophis	A, B	0 — 1.200m.
Pseudoboa	A, B	0 — 1.100m.
Pseudoeryx	A	0 — 300m.
Pseustes	A, G	0 — 2.400m.
Rhadinaea	A, G	0 — 2.100m.
Rhinobothryum	A	0 — 600m.
Sibon	A	0 — 1.700m.

<i>Generos</i>	<i>Distribucion por Tipo Climatico (KÖPPEN)</i>	<i>Niveles Altitudinales</i>
Spilotes	A, B, G	0 — 1.500m.
Stenorrhina	A	0 — 1.300m.
Tantilla	A, B	0 — 1.800m.
Thamnodynastes	A, B	0 — 2.300m.
Tripanurgos	A	0 — 1.000m.
Umbrivaga	G	+ 1.000m.
Xenodon	A, G	0 — 1.800m.
<i>LEPTOTYPHLOPIDAE</i>		
Leptotyphlops	A, B	0 — 1.200m.
<i>TYPHLOPIDAE</i>		
Helmintophis	A, B	0 — 1.600m.
Liotyphlops	A, B	400 — 1.200m.
Typhlops	A, B	0 — 1.300m.
<i>ELAPIDAE</i>		
Micrurus	A, B, G	0 — 2.500m.
<i>VIPERIDAE</i>		
Bothrops	A, B, G	0 — 2.800m.
Crotalus	A, B	0 — 2.500m.
Lachesis	A, G.	0 — 1.800m.

TOTAL: (7) Y (52) GENEROS





THE EVOLUTION OF THE VENOM APPARATUS IN SNAKES FROM COLUBRIDS TO VIPERIDS & ELAPIDS

Kenneth V. KARDONG *

ABSTRACT: The venom apparatus of poisonous snakes consists of a fang and associated venom gland (or glands). Venomous snakes evolved from nonvenomous ancestors. The course of this evolution, the adaptive advantages of the changes at each stage, and the implications of the findings to snake phylogeny, pharmacology, and clinical strategies of treatment of envenomations are the subject of this paper.

In particular, it is argued in this paper that: (1) both viperid and elapid snakes evolved from opisthodont ancestors; (2) the Duvernoy's gland in most colubrid snakes should not be seen as a gland "on its way" to becoming a venom gland, but should be examined for the immediate biological role it plays in the life of those snakes possessing such a gland; (3) it would be useful to distinguish between a property of an oral secretion (e.g. toxin) and its biological role (e.g. venom); (4) strategies of treatment of envenomation would profit if it were more fully appreciated why venom is composed of more than just a suite of toxins.

INTRODUCTION

The venom apparatus of poisonous snakes consists primarily of two components: a modified tooth, the fang by which venom is delivered into prey, and the venom gland (or glands) where toxin is produced and stored. Venomous snakes use the venom apparatus to rapidly kill prey and secondarily in defense from their own enemies.

The structure of fangs and venom glands are the subject of many revealing descriptive papers (e.g. Kochva and Gans, 1966; Rosenberg, 1967; Nickerson, 1969; Gabe and Saint Girons, 1971; Halstead et al., 1978). However, clarifying the evolution of the venom apparatus has proved to be a more contentious and elusive task (Smith and Bellairs, 1947; Kroll, 1976). In part, this arises from phylogenies of snakes constructed upon only a general or anecdotal knowledge of the functional morphology of the jaw apparatus. Thus, the first purpose of this paper is to review the functional role of both the apparatus and the evolutionary antecedents of the venom apparatus. This will lead to the formulation of focused hypotheses that yield testable predictions.

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The conclusions reached herein about the evolution of the snake venom apparatus shed a different light upon ophidian taxonomy and phylogeny, venom pharmacology, and even upon clinical treatment of snakebite. Thus, the second purpose of this paper is to discuss the implications of these conclusions for these related areas.

RESULTS

A) *Evolution of the Fang*

1. *Morphological Series*

Venomous snakes evolved from nonvenomous ancestors. Three families of snakes are immediately involved: Colubridae, Viperidae, and Elapidae (including sea snakes). Viperids and elapids are poisonous snakes with sophisticated venom apparatuses used to quickly kill prey. However, most colubrid snakes are basically nonvenomous. True, some such as *Dispholidus* seem to parallel viperids and elapids in that they possess a highly toxic venom apparatus and use it to rapidly kill prey. But, the vast majority of colubrids are truly nonvenomous.

The origin of viperid and elapid snakes from colubrids has been a longstanding concern among those interested in advanced snakes (Boulenger, 1893, 1896, 1917; West, 1895; Alcock and Rogers, 1902; Phisalix, 1912, 1922). Several relationships have been proposed. One suggests a single origin of venomous snakes from colubrids (Cope, 1900; Mosauer, 1935); another that elapids arose from opisthoglyphous colubrids, and viperids from proteroglyphous colubrids (Anthony, 1955). The relationship I use here is that both elapids and viperids evolved from opisthoglyphous colubrid ancestors, but independently (Kardong, 1980). This evolution of venomous snakes from opisthoglyphs probably occurred several times (Kochva et al., 1967; Bourgeois, 1968; McDowell, 1968; Savitzky, 1980). However, despite a lively polyphyletic origin of venomous snakes, these fall along but two pathways, one leading to viperids and viper-like snakes, and the other to elapids and elapid-like snakes. It is beyond the scope of this paper to identify how many times each of these paths was traveled by evolving snakes. Instead, the purpose is to analyze the general adaptive advantage of changes on each evolutionary highway.

If we focus our attention on the maxillary bone and the teeth it bears, then one can construct a simple morphological series (*sensu* Maslin, 1952) through which the maxilla and its teeth transform into the shortened maxilla and fang of elapids on the one hand, and viperids on the other (Fig. 1). Notice that within colubrids, there exists a range of morphological conditions. The first state, and presumably phylogenetically the most primitive, is exhibited here by *Pituophis* wherein the shaft of the maxilla is long, its teeth numerous, and the dentition basically homodont (*sensu* Edmund, 1969). In a more derived condition, as exhibited by *Dispholidus*, the maxilla is shortened, the teeth reduced in number,



and the dentition heterodont. Heterodonty is achieved by the differentiation of the posterior maxillary teeth that lengthen through this series, change shape, and eventually come to bear a groove along their sides.

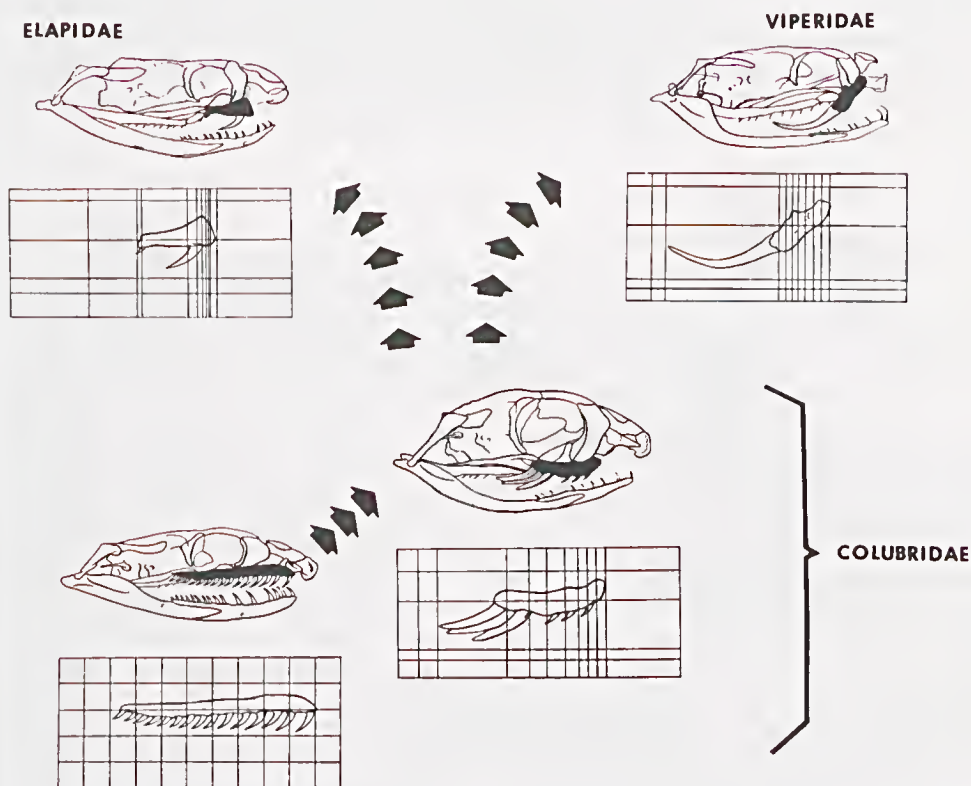


Fig. 1 — Transformation series of the maxilla and teeth it bears within the family Colubridae and to the families Elapidae and Viperidae. The rectangular co-ordinates laid over the isolated maxilla diagrammatically express changes within this morphocline. Through this series, the maxilla shortens, tooth number is reduced, and the posterior maxillary tooth lengthens. In elapids, this tooth has migrated forward to a more rostral position on the maxilla. In viperids, this tooth resides at the posterior end of the maxilla, but kinetically rotates forward during the strike. Actual skulls depicted among the colubrids are those of *Pituophis* (left) and *Dispholidus* (right). A *Naja* and *Vipera* skull represent Elapidae and Viperidae, respectively.

Evolution of the maxilla and its teeth within colubrids thus proceeds from an aglyphous to an opisthogyphous condition. Between these two extremes lie most colubrids showing graded, intermediate states. For instance, next after the initial condition would follow snakes that possessed maxillae with slightly elongated maxillary teeth (e.g. *Thamnophis*). Next would lie snakes possessing long, rear maxillary teeth, but with secretion grooves (e.g. *Crotaphopeltis*). A secretion channel too appears

in gradual stages. It would appear first, in this transformation series, as a corner between two adjacent teeth (Taub, 1967) and later as a groove within a tooth (Sarker, 1923).

This trend within colubrids to a shortened maxilla, reduced number of teeth, and elongated posterior tooth continues into the two venomous families. But, the continuation of these trends is established in two different ways. In viperids, the elongate posterior tooth (now a fang) lies at the rear of the shortened maxillary bone. In elapids, the elongated posterior tooth (now also a fang) lies not at the rear of the shortened maxillary bone, but forward on the remaining shaft. Occasionally, small teeth remain at the posterior end of the elapid maxilla marking the point at which the fang once resided in elapid ancestors.

2. Adaptive Advantages

a) Accretion Hypothesis

A common view holds that these evolutionary changes in the maxilla and its teeth are driven by the increasing and additive advantages long teeth serve in venom injection. Thus, by the accretion of progressive toxic benefits, a venom system develops. This hypothesis predicts that the initial and the subsequent role played by these teeth was in prey capture.

To test this prediction, several living species (*Thamnophis*, *Crotaphopeltis*) falling within the middle stages of the transformation series among colubrids were examined to see just how they used their maxillae and posterior maxillary teeth. These species possess long posterior maxillary teeth. The results (Kardong, 1979, 1980; Wright, *et al.*, 1979) showed that, in fact, they did not use these teeth extensively during prey capture. Instead, they used these teeth to manipulate prey once already caught (see also Minton, 1944; Platt, 1969; Kroll, 1976). Thus, these teeth, even though slightly elongated, did not serve to inject a venom during prey capture, but instead aided swallowing by acting like small hooks to give better purchase on the slippery or uncertain surface of the prey. Further, comparison of the posterior maxillary teeth and of a venom fang revealed that the two are quite unlike (Schaefer, 1976; Kardong, 1979; Wright *et al.*, 1979).

Thus, no support was found for the predictions of the accretion hypothesis, at least as applied to snakes within the middle of the transformation series.

b) Deglutition Hypothesis

Alternatively, I propose (Kardong, 1979; 1980) that these teeth borne by maxillary bone initially functioned as hooks or gaffs to improve purchase during swallowing. This role favored, (1) elongation of the teeth, and (2) shortening of the maxillary bone, two changes, in fact, present in the jaws of many colubrid snakes. Once long teeth along the maxillary bone had arisen to serve the requirements of swallowing, then they would be preadapted to subsequent evolution into a new function, that of venom injection. But, the *initial* adaptive advantage of long maxillary teeth was not related to venom injection, but instead to swallowing.

B) Evolution of the Venom Gland

1. Morphological Series

The evolution of the venom gland, like the previous evolution of the fang, begins within colubrid snakes. Within colubrids, the Duvernoy's gland is the evolutionary predecessor of the venom gland (Gans and Elliott, 1968; Kochva, 1978). A morphological series constructed now for the Duvernoy's gland shows its transformation into the venom gland of viperid and of elapid snakes (Fig. 2).

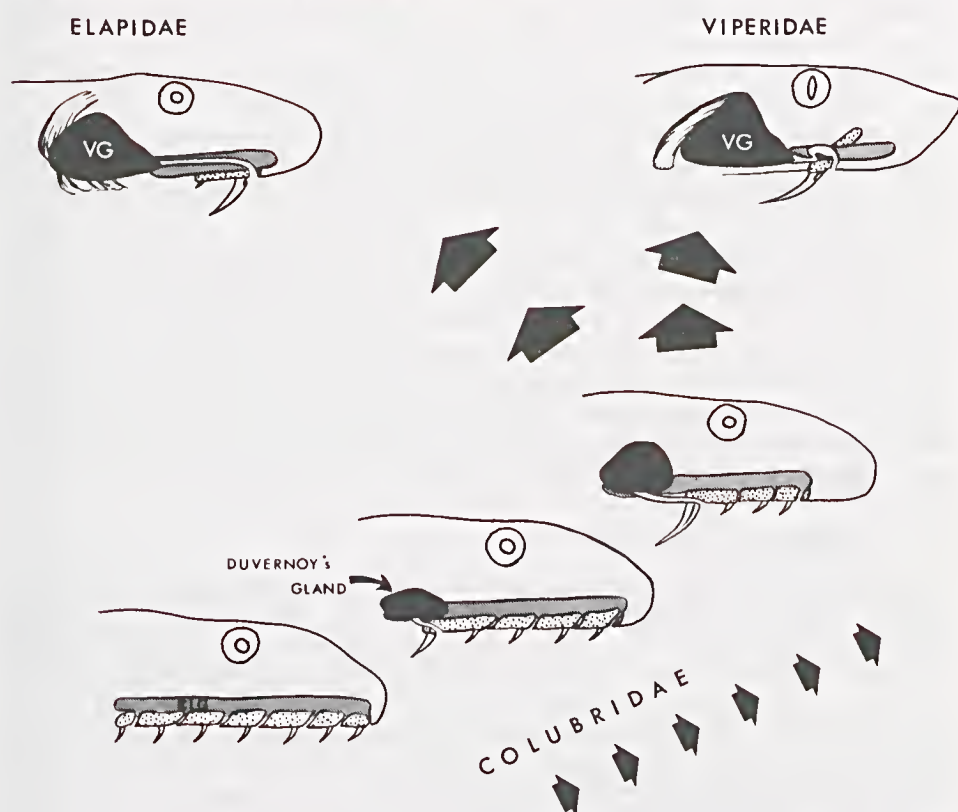


Fig. 2 — Transformation series of Duvernoy's gland. This gland appears first within the middle of the colubrid series. It arises near the posterior end of the supralabial gland (SLG). Through the morphocline, the Duvernoy's gland transforms independently into the venom gland (VG) of elapid and viperid snakes.

2. Adaptive Advantages

a) Accretion Hypothesis

Again, the conventional view is that the Duvernoy's gland was always slightly venomous and that the increasing, additive advantages of venom injection drove the changes leading eventually to appearance of a fully venomous gland. But, again there is reason to doubt this hypothesis. First, as just mentioned, even though the teeth of colubrids

are long, they are otherwise structurally quite unlike fangs. Second, most colubrid snakes do not have large storage areas to hold venom (Taub, 1967) to inject and rapidly kill prey.

Further, those who subscribe to this accretion hypothesis face a self-imposed paradox, what may be termed the "paradox of imperfection". By the accretion hypothesis, possessors of a Duvernoy's gland are "on their way" to becoming highly venomous, but, as yet, possess only a mild venomous capacity. But, in fact, most living colubrids are so endowed with long, posterior maxillary teeth (Marx and Rabb, 1972) and a Duvernoy's gland (Taub, 1967). In most parts of the world, such colubrids live sympatrically with and outnumber in terms of species, venomous snakes such as viperids and elapids. The paradox lies in the fact that such colubrids with a presumed mildly venomous secretion, but "imperfect" venom apparatus, could be so successful with these two families that possess a highly venomous and efficient venom apparatus. It does seem contradictory that colubrid species could compete and thrive using an "imperfect" venom injection system as successful contemporaries with elapids and viperids.

Perhaps, I have overstated or misstated the paradox. On the other hand, the paradox may arise from a flawed hypothesis, the accretion hypothesis. Tris, in fact, is my view. Most colubrids simply do not seem to use their oral secretions as venoms. Eventhough the oral secretions of many colubrids are proving to be more toxic than previously suspected (McAlister, 1963; Heatwole and Banuchi, 1966; Vest, 1981), still these same species do not, in fact, use their oral secretions to rapidly kill prey as do truly venomous snakes possessing fangs.

2. *Deglutition Hypothesis*

Duvernoy's gland secretion (in most colubrids) serves not as a venom. This is to say, it does not serve to help rapidly kill prey during prey capture. Instead, it must serve some other primary biological role or roles for these species. Being associated with the swallowing behavior of snakes, the secretion of Duvernoy's gland may reasonably be expected to play a role in swallowing and/or digestion. However, without further broad study of both the pharmacology of Duvernoy's gland secretions together with studies of the feeding behavior, it is premature to propose any careful alternative hypothesis.

CONCLUSIONS

Early in the evolution of the venom apparatus among snakes, the posterior maxillary teeth were long, but not yet fangs. Instead they served as spikes to help the snake grip slippery, bulky, or difficult prey during swallowing. So too, the Duvernoy's gland was not yet a venom gland, but likely served some other biological role.

Certainly once these teeth were long and the Duvernoy's gland well established, then this system was preadapted for the quite different role

of quickly subduing prey. Later in its evolution, the tooth/gland system then evolved under the increasing advantages derived from the ease and efficiency of rapidly killing prey. But, prehension and envenomation were not the *initial* roles that drove the early evolution of the glandular and dental elements in the jaws of colubrid snakes toward long, posterior teeth on a shortened maxilla.

IMPLICATIONS

A) Snake Evolution

1) *Viperidis and Elapids - two venom modes*

Both viperid and elapid snakes evolved independently from opisthognath ancestors. At least, this is the view I take based upon the arguments presented herein. The alternative view that elapids (or viperids) arose from proterognath ancestors is contradicted by the position of the venom gland (McDowell, 1968), embryonic development (Martin, 1899a,b,c; Kochva 1963; 1965), and rear maxillary tooth structure, position, and function (Kardong, 1980:273-274).

Upper jaw teeth in colubrids serve in two primary capacities—prehension and swallowing. But, these two activities are not always shared equally among the teeth. Anterior teeth of the mouth tend more often to be involved in prehension because they are first to come into the vicinity of the prey and because they bear responsibility for snagging elusive prey. Correspondingly, anterior teeth are often long and recurved reflecting their special role in prey capture (Frazzetta, 1966). Posterior teeth, on the other hand, tend to be involved in preingestion/swallowing manipulations. Because of the kinetic motion of the maxilla, rear teeth it bears lie at an especially favorable mechanical position to aid in swallowing (Kardong, 1979). Consequently, posterior maxillary teeth are often long and blade-shaped (Wright *et al.* 1979).

The fang borne by the maxilla in elapids and viperids is, like anterior teeth of colubrids, deployed principally during prey capture. It is thus fashioned similarly. For instance, the fang is conical and often recurved (Klauber, 1956); it is located, during the strike, in the anterior part of the mouth. In this latter feature, however, this forward position in the mouth is accomplished in two different ways. In viperids, the fang rides upon a highly kinetic maxilla that erects during the strike to bring the fang well forward in the mouth (van Riper, 1953; Kardong, 1975). In elapids, the fang rides on a less kinetic maxilla, but has undergone during its evolution a forward migration so that it sits in a more anterior position along the shaft of the maxilla (Fig. 1). Thus, fangs in the two groups enjoy the advantages of an anterior position in the mouth, but this is achieved differently—phylogenetic migration along the maxilla in elapids, kinematic rotation in viperids. Although elapids and viperids are venomous snakes, they seem to be separately derived styles of a venomous mode of life. They differ in the structural features of the

maxilla and fang just mentioned, relative toxicity of their venoms (e.g. Minton and Minton, 1969), and perhaps even in behavioral styles in their strategies of prey capture (Nauulleau, 1965; Kardong, 1982).

2) *Duvernoy's gland*

The Duvernoy's gland in most colubrid snakes is unlikely a gland "on its way" to being a venom gland, but should be examined for the immediate biological role it plays in the life on those snakes possessing such a gland.

B) *Pharmacology*

1) *Toxin and Venom*

A distinction should be made between a secretion that is a "toxin" and one that is a "venom", at least as applied to snake secretions in a biological context. These two terms have grown up in the medical literature with closely related meanings (e.g. Russell, 1980). I don't intend to propose redefinition in a medical or clinical context. However, the transference of these terms into a biological context has led to confusion. As a result, some animals live with an undeserved reputation for danger and even some medical strategies of treatment of suspected envenomations suffer from the confusion.

In a biological context, by "toxic" I mean the lethal *property* of a chemical expressed as an LD₅₀ or LD₁₀₀, for example; it is usually identified and characterized under defined laboratory conditions. However, by the term "venomous" I mean the *function* of the secretion, specifically the biological role (Bock, 1980) of the substance in the life of the animal producing it. Observation of the free ranging animal in its natural habitat is usually or ideally the basis for concluding (or not) that a secretion is used as a venom. The two terms rest on different concepts so more is at issue than mere semantics.

If Duvernoy's gland secretion is shown to be toxic, some suggest from this alone that the snake is likely venomous. However, there are two reasons for resisting such a hasty conclusion.

2) *Incidental Byproduct*

First, to prove a substance toxic in character is insufficient to prove it venomous in practice. Toxicity can occasionally be an incidental byproduct. For example, some components of human saliva are toxic and possess an LD₅₀ (Bonilla *et al*, 1971). Yet, no food humans consume require envenomation to make it safe to eat, nor are there enemies thwarted by threat of saliva injection. Toxicity is incidental and those seeking the biological role of saliva look, quite rightly, beyond this property to its digestive roles to understand its chemical character. However, analysis of oral secretions from "nonvenomous" snakes has not always been so sensible. Too often, only the property of toxicity of these secretions seems to have been seriously considered. Certainly, this

is understandable. Lethal dose, if any, can be relatively easily demonstrated, and hence toxicity discovered; also, the toxicity alone makes the substance medically important regardless of its actual biological function. Yet, in many colubrid secretions, toxicity might be, as with human saliva, incidental, a property with no or only secondary biological significance. It would be misleading to call humans "venomous" simply because they possessed a "toxic" saliva. Similarly with snakes. In a biological context, distinguishing conceptually between a toxin and a venom should help avoid such confusion.

3) *Other Functions*

There is a second reason for resisting the temptation to conclude that a toxic secretion is also automatically a venom. In most colubrids, Duvernoy's gland secretion functions in capacities other than as a venom. Many colubrids possess well developed Duvernoy's glands, yet do not use its secretion to rapidly kill prey. To take an example, the wandering garter snake (*Thamnophis elegans*) possesses a Duvernoy's gland secretion of alarming toxicity approaching that of some viperid snakes (Vest, 1981; 1982), yet lacks the teeth to inject much secretion (Wright *et al.*, 1979), and does not feed by bringing rapid death to the prey (Peterson, 1978). It possesses the toxicity, but lacks the equipment and behavior to use the secretion as a venom. The secretion from Duvernoy's gland or, for that matter, any secretion released from a specialized organ or group of cells may serve several functions. It may function as a venom, it may paralyze prey, it may tranquilize, it may aid digestion, and so on. In *Thamnophis* and similar colubrids, what then could be this secretion's function?

4) *Alternative or Additional Functions*

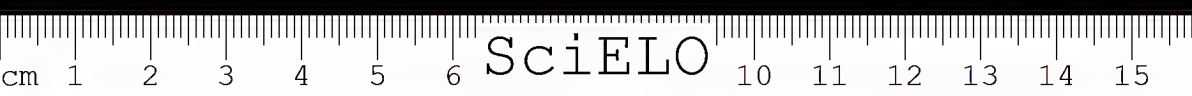
To date pharmacological and biological analysis of Duvernoy's gland secretion has been preoccupied with toxicity (e.g. Philpot *et al.*, 1977), so one is left to speculation about alternative functions. However, several seem likely.

a) *Lubrication*

Besides Duvernoy's and venom glands, snakes possess additional strips of glandular tissue along upper and lower lips (Taub, 1966) that release their products over the prey to lubricate its passage into the esophagus. Duvernoy's gland secretion, released at the base of rear maxillary teeth, trickles down the sides of these teeth to likely finds its way to the surface of the prey. Thus it could be an additional source of lubricant to facilitate swallowing.

b) *Digestion*

In viperid and elapid snakes, venom certainly contributes to rapid prey death, but has also been suspected of promoting digestion (Reichert, 1936; Zeller, 1948). Experimental work — injecting venom into mice and then comparing rates of their digestion to controls — indicates that rattlesnake venom actually speeds digestion (Thomas and Pough, 1979).



Such venom attributes may be of adaptive value for snakes feeding on large numbers of prey in short periods of time or to enhance digestion in snakes from cold or temperate climates. Similar tests have not been done for the secretion from Duvernoy's gland, but the possibility it serves a similar function seems worth investigating.

c) *Anti-putrefaction*

Snakes swallow their food without tearing or chewing. Digestive enzymes released from the wall of the gut may not always complete the inward spread of digestion before tissues within the center of the bolus putrefy. Venom injected deep (Thomas and Pough, 1979) or Duvernoy's gland secretion inoculated subcutaneously within the prey before swallowing may retard this putrefaction.

d) *Detoxify Prey Secretions*

Many snakes, especially colubrids, feed on amphibians possessing skin glands which contain, depending upon the amphibian species, irritating to actually poisonous secretions (Habermeihl, 1971; Lutz, 1971; Brodie and Tumbarello, 1978). Duvernoy's gland secretion in those colubrids regularly feeding on amphibians may help neutralize these skin secretions released by the amphibian prey.

Further, these oral secretions could contribute to improved oral hygiene or prevent sticky material elaborated by prey from fouling the jaws during swallowing (Gans, 1978; Jansen, 1982). My intent is not to settle the questions of what functions snake oral secretions serve. Instead, I wish to emphasize that snakes, faced with a variety of problems while catching and swallowing prey, might possess various components in the Duvernoy's gland or venom gland secretions that serve a variety of biological roles besides or in addition to envenomation.

Even though introduced into the prey in small quantities compared to a true venom, some propose that the Duvernoy's gland secretion may slow or tranquilize the prey, thus making prey capture less risky and swallowing easier. Perhaps it does. But, tranquilizing prey differs from envenomation. Tooth form (Kardong, 1979; Wright *et al.*, 1979), maxillary bone structure (e. g. Bogert, 1943; Brattstrom, 1964), and behavior (e.g. van Riper, 1953; Klauber, 1956; Dullemeijer, 1961; Greene and Burghardt, 1978) differ from species that use venom predominantly to capture and dispatch rather than just quiet prey. Consequently, tranquilization seems distinct from true envenomation as a prey handling technique.

C) *Clinical Significance*

Venomoses are complex. Laboratory analysis proceeds by fractionation into molecular components then to separate analysis of each fraction. Some components exhibit toxicity while other components seem to be without toxic effect (e.g. van Mierop, 1976; Russell, 1980). These nontoxic fractions are usually classified as potentiators, activators, or amplifiers (e.g. spreading factors) of the toxic components. Generally this conclusion seems on mark. However, some of these components of venom may lack toxicity, because they are present for biological reasons other than to

promote rapid prey death (e.g. Thomas & Pough, 1979). In fact, even demonstrating toxicity in a particular component does not or ought not to end the search for its possible function. Other attributes, besides toxicity, should be considered if one is to eventually understand the biochemical action and interaction of all venom components.

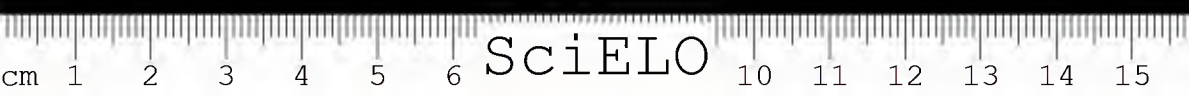
One fruitful place to begin such an analysis may be with the secretion from Duvernoy's gland. The venom gland of viperids and elapid snakes evolved from the Duvernoy's gland; these venomous snakes feed upon similar foods and thus face generally similar problems with prey as many "nonvenomous" colubrids. Certainly the venom of viperids and elapids functions primarily to rapidly kill prey, but components serving secondary functions are most likely present as well. Venom is a suite of chemicals, all of which go into a victim — toxins and nontoxins alike. Consequently, it seems advisable for strategies of treatment of envenomations to be founded upon a knowledge of all components and their biological roles, not just upon the action of the toxins. Perhaps, somewhat ironically, one place to focus such an analysis of snake venoms, is on "nonvenomous" colubrid snakes.

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METHODOLOGY APPLIED IN THE ELABORATION OF FAUNAL SALVAGE IN THE REGION OF "AGUA VERMELHA" HYDROELECTRIC POWER PLANT. CENTRAIS ENERGÉTICAS DE SÃO PAULO — CESP

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ABSTRACT: This paper describes the planning of the faunal rescue operation in areas destined for great reservoirs for hydroelectric power plants in Brazil. An extensive study was elaborated of the topography (forests, plantations), eventual formation of islands through the rising of water, inquiry into species of animals, mainly snakes, there existing. Division of the whole area in sectors for better realization of the work. Selection of adequate sites for the installation of antiophidic stations (maximal distance — 3 h). Training of the boat and vehicle crews. Informative lectures to all participants, official staffs of the different municipalities, and florestal police on measures to be taken. The number of animals rescued, and returned to nature at appropriate places in the vicinity, justifies the extensive action.

INTRODUCTION

Induced by the growing need of new sources of energy, man have continuously impaired the environment — in Brazil mainly through the construction of great reservoirs for hydroelectric power plants — in such a way that the deep apprehension as to future incidents is not exaggerated. Alterations produced by man-made lakes demand early analysis and evaluation so that the biological system can be preserved as far as possible, since drastic ecological changes never were beneficial to man.

The increasing ecological consciousness invoked extensive studies related to the damaging effects on the environment, that eventually may mitigate the expected adverse impact by the projects accompanied by needless destruction of natural riches.

Papers with reference to studies on the environment by Machado (1974, 1975), Cornaby (1978), the ecological survey recommended by

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Goodland (1977), faunal inventory preconized by Coutinho (1978), Coutinho et al, (1979), evidence that in fact the ecological conscience is being excited in Brazil as in the rest of the world (Garcez, 1978).

Motivated by the obligation to help as much as possible in the protection of wildlife, this marvelous bequest of nature to mankind, that must be preserved at any cost for future generations, the joint team ZOO-BUTANTAN collaborated with "Furnas Centrais Elétricas" during the closing of the "Marimbondo" barrage, were steps of anticipated planning and installation of antiophidic stations were in fact applied for the first time, and later similar collaboration was given to ELETROSUL in "Salto Osório", ELETRONORTE in "Coaracy Nunes", and CESP in "Capivara", results of which are discussed in the paper by Belluomini, Cembranelli and Autuori (1976/1977).

The planned faunal rescue at the site of the hydroelectric power plant of "São Simão", designed according to CEMIG (1979) has been executed by the staff of the proper Centrais Elétricas de Minas Gerais.

"Itaipu Binacional" (1979) promoted the Ist. Seminary on Environmental Preservation, manifesting through technical papers published in a special volume particular attention to the protection of the environment and future faunal rescue.

ELETROSUL in "Santo Santiago", and COPEL in "Foz de Areia", developed intense studies of technical-scientific nature, preparing in advance the faunal preservation and rescue on occasion of the filling of the reservoirs in 1979 and in 1980. "Furnas Centrais Elétricas" made arrangements for the rescue operation in "Itumbiara", 1979, based on the ecological study of the UFMG (1976).

The work referring to the rescue and replacement of the ichthyological fauna, downstream as well as upstream, constituted the responsibility of specialists as Machado and Alzuguir (1976), and Paiva (1978).

CESP through Dr. Cirilo Eduardo Mafra Machado, Administrator of the Environmental Department, asked for the collaboration of the joint team ZOO-BUTANTAN in "Água Vermelha".

The present paper describes the methodology for a project of faunal rescue and preservation, comprehending antecedent planning, programming, and training of personnel, improving the achievements in other hydroelectrics.

The rescue operation executed from 26-6-78 to 11-8-78, was conducted by the proper Hydroelectric Company under the general coordination of the resident engineer Walmir Fernando Modesto with the collaboration of the joint team ZOO-BUTANTAN.

As to the Health and Sanitation Program, CESP (1978 *a*) received full collaboration of the Superintendency for Endemic Control from the Division of Health of the São Paulo State. Countless studies on sanitary aspects can be found in the literature (Deom, 1976). Intense studies in this sense are being conducted by Itaipu Binacional in the inundation area and vicinity, results of which are published in the 1st Volume of the "1er Seminario de la Itaipu Binacional sobre Medio Ambiente", 1979.

LOCALIZATION

The hydroelectric power plant of "Água Vermelha", property of the Centrais Energéticas de São Paulo — CESP — (Fig. 1), situated at the "Rio Grande", boundary of the São Paulo and the Minas Gerais States, was constructed in the region of the waterfall "Cachoeira dos Índios", later disappearing with the rise of the water, and 80 km distant from the confluence of the "Rio Grande" with the river "Parnaíba". The extension of the reservoir is of 168 km, and the area of the hydrographic basin 139 900 km², an area of 650 km² of the total reservoir, a volume of 11 billions m³ of accumulated water, and 1380 MW of energy to be gerated (CESP, 1978 a).

INSPECTION OF THE IMPOUNDMENT AREA

Early in April, 1978, technicians of the joint team, Hélio Emerson Belluomini, Med. Vet. (Inst. Butantan), Ladislau A. Deutsch, Biologist-Zoo de São Paulo, and Luiz F. Galli, Florestal Engineer (CESP) conducted a reconnaissance of the whole impoundment area by helicopter, boat, and vehicle. The main purpose was to evaluate, as regard faunal rescue, the type of basin involved, forests, areas of plantations and pastures, estimate the density of local fauna, select faunistic refuges for future biological control, installation of antiophidic stations, availability of antiophidic sera in drugstores and hospitals in adjacent cities.

The aerial and terrestrial survey showed that the left border of the river is more elevated and would, at least inically, determine minor inundation areas, with progressive rising of the water without major problems; a great part of this region is constituted by pastures and annual cultures, mainly soja, less cotton and maize.

Besides the exuberant riparian ciliate forest, several arboraceous sites were noted, which at first sight seemed to be formed by vestiges of primary forest in an extension varying from 48.4 ha to 145.2 ha. These wooded regions will not become flooded, and 2/3 of the largest arboreous part will be bordered by the new lake, however will not present major problems during the rising of the water up to the maximal inundation quota.

The topography of the region shows that two islands are going to be formed by the rising water, one situated between the "Ribeirão Lajeado" and the "Ribeirão Água Vermelha" rivers, and the other between the "Aroeira" and "Maravilhas" rivers.

The riparian region on the right side presents a less expressive ciliar forest; the probable formation of an island of about 40 ha can be expected at the maximal inundation quota. The already existent islands will submerge. The territory is more plane and less elevated, involving greater impoundment areas, and according to the aerial survey, part of the forest not yet cut down, will submerge without the formation of islands. Cultivated areas or pastures are seen, although in less a scale than on the left border. Pastures predominate, and then maize and cotton plantations, deserving special attention with regard to the presence of snakes.

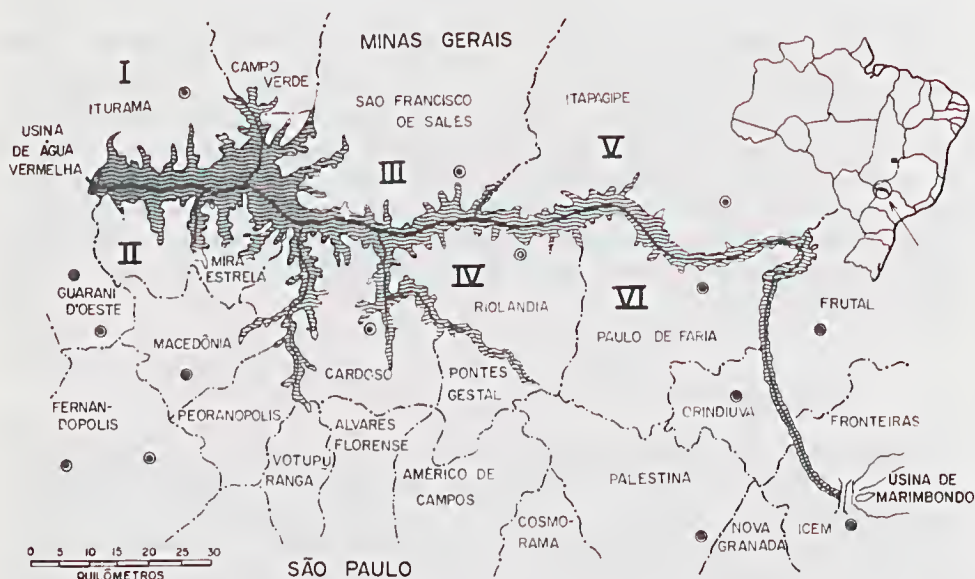


Fig. 1 — Map — localization of the reservoir destined for the hydroelectric power plant "Água Vermelha". Division of the area into the rescue regions I-VI, and indication of antiophidic stations.

Antiophidic Stations — Boat crews

Coordinator of the faunal rescue operations: Pedro Castelo B. Rosário (CESP)

Aides: Giuseppe Puerto (biol. — Inst. Butantan)

Antonio S. Martins Rodrigues (biol. — FPZSP)

Auxiliary: Oscar da Silva

N.º 1 region

Officer on duty: Antonio G. Real (CESP)

Boat crew: Fernando C. Rodrigues (CESP), Maurício T. de Lima (*), and 1 Military Policeman (PM).

Antiophidic Station: a — Hospital e Maternidade Santa Rosa — Dr. Antonio J. Monteiro Gama; b — Unidade de Saúde de Iturama — Dr. Sérgio da Cunha Garcia.

N.º 2 region

Officer on duty — Vandir Dias (CESP)

Boat crew: Abelar R. da Costa (CESP), Israel M. Bleich (*), and 1 PM.

Antiophidic Station: Hospital CESP de Indiaporã — Dr. Arrigo Maiolini Junior, and Dr. Kenichi Akimura.

N.º 3 region

Officer on duty: Sandoval O. de Lima (CESP);

Boat crew: Celso A. de Oliveira (CESP), Luiz E. de Melo M. Machado (*), and 1 PM.

Antiophidic Station. Posto de Saúde de São Francisco de Sales — Dr. Joaquim E. Camargo.

N.º 4 region

Officer on duty: Aldebrando H. da Silva (CESP);

Boat crew: Antonio R. do Prado (CESP), Luiz E. M. de Vasconcelos (*), and 1 PM.

Hospital on duty: Hospital e Maternidade Leonor Mendes de Barros — Dr. Leovaldo Canoas.

N.º 5 region

Officer on duty: Clarindo Qu. da Silva (CESP);

Boat crew: Paulo E. Pereira (IB), and 2 PM.

Hospital on duty: Casa de Saúde e Maternidade de Itapagipe — Dr. Edimar Silva Machado.

N.º 6 region

Officer on duty: José P. da Silva (CESP), and 3 PM.

Antiophidic Station — Pronto Socorro Municipal de Riolândia — Dr. Osvaldo de Paiva, and Santa Casa de Misericórdia de Paulo de Faria — Dr. João A. M. Casarini.

Two auxiliary boats participated also in the operation, each with 3 PM.

Siglas: CESP — Companhia Energética de São Paulo

IB — Instituto Butantan

FPZSP — Fundação Parque Zoológico de São Paulo

* — Students of the Faculty of Veterinarian Medicine aggregated to the Inst. Butantan team

PM — Florestal Military Police of Natural Resources.



70% of the economical activities of the region to be flooded (CESP, 1978 a) concentrate toward cattle raising and agronomics; 20% were distributed in the municipalities of the São Paulo State (Indiaporã, Mira Estrela, Macedonia, Cardoso, Riolandia, and Paulo de Faria) with 3,488.50 ha of maize, rice, cotton, and soy plantations; on the side of the Minas Gerais State, the municipalities to become affected (Iturama, Campo Verde, São Francisco de Sales, Itapagipe, and Frutal) comprehend 2,143.8 ha of maize, rice, cotton, soy and peanut plantations.

CESP organized a special team to penetrate the woodland not to be deforested, since experience shows that animals tend to leave areas invaded by man. This means that 6,700 ha of woodland have to be scoured periodically in an attempt to promote exodus of the animals to other regions.

INSPECTION — FAUNA OF THE REGION

CESP (1978 a) made a detailed inspection of the whole area to be flooded in search of wild animals, allowing the elaboration of the following list of mammalian species: *Cerdocyon thous* (Linnaeus, 1766); *Tayassu tajacu* (Linnaeus, 1758); *Hydrochoerus hydrochaeris* (Linnaeus, 1958); *Dasyprocta azarae* (Lichtenstein); *Callithrix jacchus penicillata* (Hershkovitz, 1968); *Cuniculus paca* (Linnaeus, 1758); *Nasua nasua* (Linnaeus, 1758); *Tayassu albirostris* (Illiger, 1811); *Tolypeutes matacus* Desm., 1804 or *T. tricinctus* (Linnaeus, 1758); *Priodontes giganteus* (Goef., 1803); *Mazama gouazoubira* (Fischer, 1814).

The scientific names were supplied by the biologist L. A. Deutsch, Division of Mammals from the ZOO, who gave also the list of other eventually existing mammals in the area of the future reservoir of "Água Vermelha" such as: *Cavia aperea* (Erxleben, 1777); *Coendu prehensilis* (Linnaeus, 1758); *Sylvilagus braziliensis* (Linnaeus, 1758); *Cebus* sp.; *Alouatta caraya* (Humboldt, 1812); *Dasyppus novemcinctus* (Linnaeus, 1758); *Euphractus sexcinctus* (Linnaeus, 1758); *Tamandua tetradactyla* (Linnaeus, 1758); *Didelphis aurita* (Wied, 1826); *Didelphis marsupialis* (Linnaeus, 1758).

The technicians of the "Departamento de Meio Ambiente da CESP" made also a survey of the ornithological population of the region; the ichtyological survey, including an inventory of the species, transference of fishes from downstream to upstream, constituted the responsibility of the specialist Cirilo M. Machado, CESP.

During the period of inspection, the trained personal of the hydroelectric company, captured the following ophidic species, which were classified according to Peters and Orejas Miranda (1970), and Hoge & Romano (1972): *Bothrops moojeni*, the most frequent venomous species present in the various regions of this hydroelectric reservoir; *Bothrops alternatus*; *Crotalus durissus terrificus*, and from the non venomous species: *Chironius* sp., *Helicops* sp., *Mastigodryas* sp., *Boa constrictor* sp., *Waglerophis merremii*; 2 specimens of *Eunectes* sp. were seen but not captured.

MATERIAL

The material used for the faunal rescue operation was manufactured in the work-shop of the proper CESP, including the standard model from the Instituto Butantan. Figs. 2-9 show the general measurements.

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Fig. 2 — Photo CESP — Cage with 4 partitions for mammals, devised by the joint team CESP-ZOO-Butantan

General measurements

hight 1.05 m
width 1.05 m
depth 0.85 m

Trap door

hight 0.8 m
width 0.44 m

Mesh 5 x 5 mm

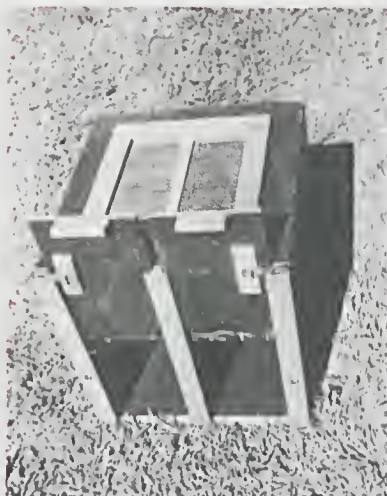


Fig. 3 — Photo CESP — Cage with 2 partitions for the transport of ophidians and mammals, devised by the joint team CESP-ZOO-Butantan.

General measurements

hight 0.61 m
width 0.61 m
depth 0.61 m

Trapdoor

hight 0.35 m
width 0.25 m

Air hole

0.32 x 0.32 m

Mesh 5 x 5 mm

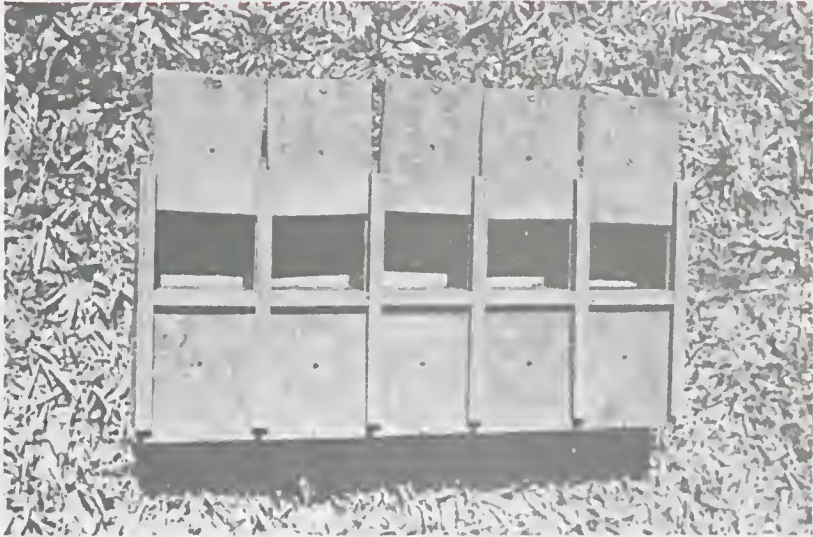


Fig. 4 — Photo CESP — Box with 10 partitions for the transport of arachnids, and small ophidians, devised by the team CESP, ZOO, BUTANTAN.

General measurements

hight	0.09 m
width	0.50 m
depth	0.25 m
opening	0.09 x 0.12 m

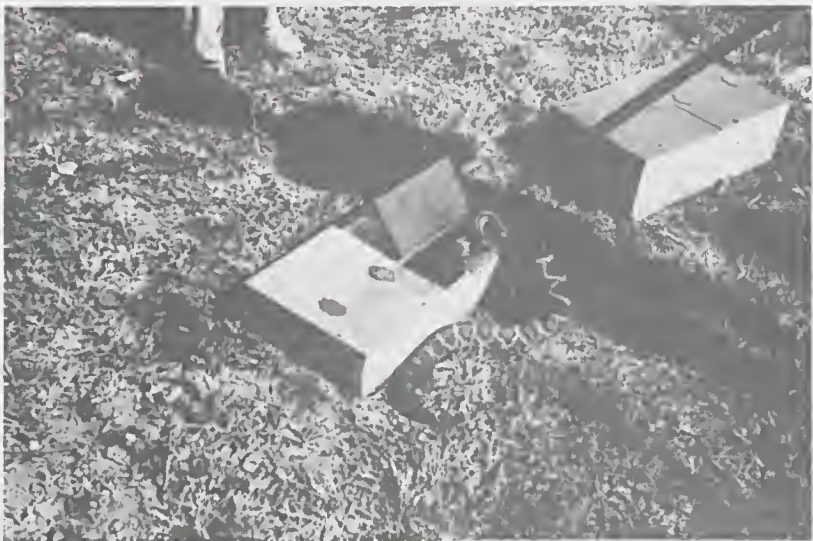


Fig. 5 — Photo Inst. Butantan — Box with 2 partitions for the transport of ophidians, standard model of the I.B.

General measurements

hight	0.12 m
width	0.50 m
depth	0.29 m
opening	0.25 x 0.12 m

A first aid manual for the treatment of individuals accidented by venomous animals was elaborated by the medical team (João L. Costa Cardoso — Hospital "Vital Brazil", Instituto Butantan, and Ernesto H. Miyauchi — Head of the Medical Department of CESP) (1978 *b*), containing specific instructions (roads, airfields, list of hospitals, addresses of physicians and nurses) for each of the areas, determining the amount of sera necessary for each of the antiophidic stations.

According to the planning, CESP decided to invite the Natural Resource Police Force of the São Paulo and the Minas Gerais States to assist the boat crews engaged in the animal rescue, to reinforce the inspection of the borders, patrol the region to impede ruthless hunters, trying to take advantage of the situation, decimating a great part of the game. The designated militars received also a general training.

Addresses were given to authorities of the municipalities within the area of "Água Vermelha", comprising sanitarians, mayors, aldermen, engineers, biologists, pharmacists, veterinarians, teachers of the 1.^o and 2.^o degree, and civil and military entities, about the planning related to the filling of the barrage, and the measurements to be adopted for environmental preservation.

Authorized by CESP, several veterinary students from the University of São Paulo participated as volunteers in the operation, and were previously trained by the Instituto Butantan and ZOO; graduated technicians of "Itaipu Binacional", two Paraguayans and two Brazilians, also participated, since similar problems are expected during the filling of the Itaipu reservoir.

PLANNING

A map of the entire area of the future reservoir was elaborated, delimiting six independent regions, of which N.^o 1, 3, and 5 are situated on the right border (Minas Gerais State), and N.^o 2, 4, and 6 on the left border of the river (São Paulo State).

The N.^o 1 region comprehends the Iturama area; N.^o 2, the Indiaporã municipality; N.^o 3, São Francisco de Sales; N.^o 4, Mira Estrela and Cardoso; N.^o 5, Itapagipe, and finally N.^o 6, the municipalities of Riolandia, and Paulo de Faria. Each of the regions would be self-sufficient as to motor boats, vehicles, radio communication, collecting equipment, repair shops, fuel and depots for diverse materials. Each of these regions received detailed maps indicating available roads that can be used at even the most adverse climatic conditions, the localization of airfields with the number of available airplanes, estimate of hours for the utilization of one or two helicopters, distance to be overcome in each of the autonomous regions; location of day and night attendance by physicians and nurses on duty in hospitals or at mobile stations (vehicles), antivenins in stock (antiophidic, antiarachnidic sera) necessary at each station, and general radio-communication control (CESP, 1978 *b*).

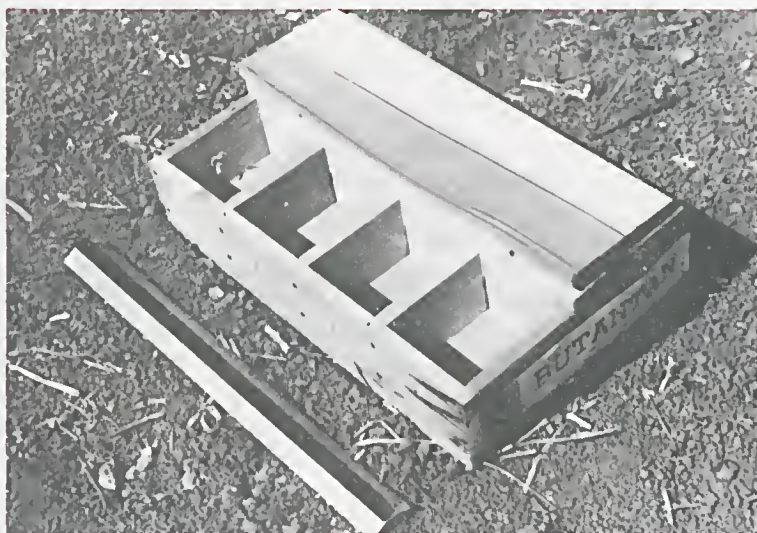


Fig. 6 — Photo Inst. Butantan — Box with 8 partitions for the transport of arachnids, standard model of the Inst. Butantan.

General measurements

high 6.8 cm
width 18 cm
depth 30 cm
opening — length 6.5 cm — width 7.5 cm — hight 4.5 cm

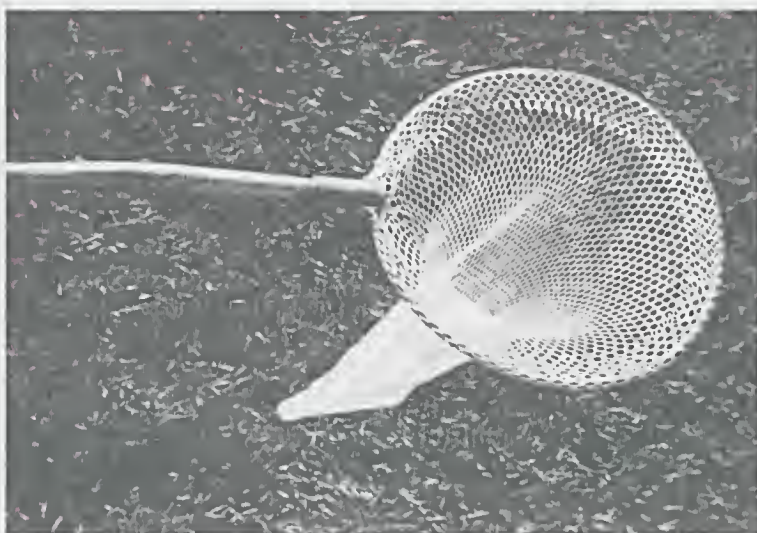


Fig. 7 — Photo CESP — Netbag to catch mammals.

General measurements

diameter	N.º 1	N.º 2
hoop	0.48 m	0.26 m
handle	0.30 m	0.30 m
length	N.º 1	N.º 2
handle	1.50 m	1.50 m
net	0.60 m	0.50 m
mesh	10 x 10 mm	10 x 10 mm

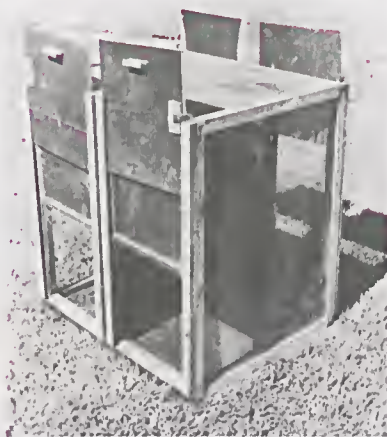


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General measurements

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Trap door

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width 0.44 m

Mesh 5 x 5 mm



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depth 0.61 m

Trapdoor

height 0.35 m
width 0.25 m

Air hole

0.32 x 0.32 m

Mesh 5 x 5 mm

BELLUOMINI, H. E. & AUTORI, M. P. Methodology applied in the elaboration of faunal salvage in the region of "Água Vermelha" hydroelectric power plant. Centrais Energéticas de São Paulo — CESP. *Mem. Inst. Butantan*, 46:119-138, 1982.

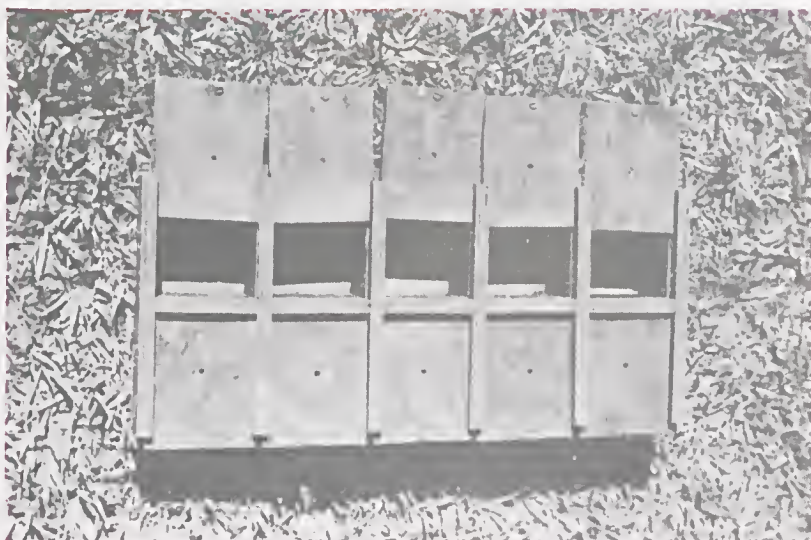


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opening	0.09 x 0.12 m



Fig. 5 — Photo Inst. Butantan — Box with 2 partitions for the transport of ophidians, standard model of the I.B.

General measurements

hight	0.12 m
width	0.50 m
depth	0.29 m
opening	0.25 x 0.12 m



Fig. 8 — Photo Inst. Butantan — Hook to catch snakes, standard model of the Inst. Butantan.

General measurements

<i>Diameter</i>	
metal	0.6 m
handle	0.30 m
<i>length</i>	
handle	1.00 m
hook	0.15 m

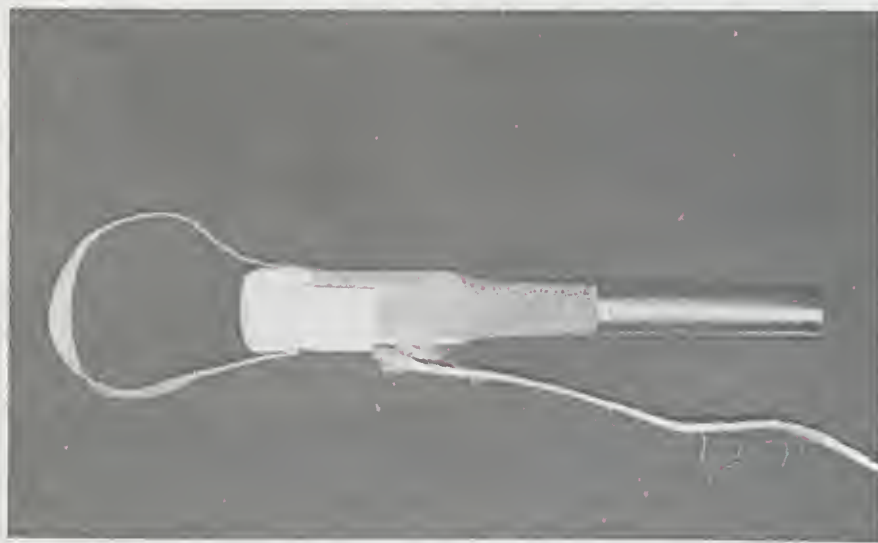


Fig. 9 — Photo Inst. Butantan — "Lutz's lariat to catch snakes, standard model of the Inst. Butantan.

General measurements

<i>Diameter</i>	
handle	0.30 m
lariat	0.11 m
<i>length</i>	
handle	1.50 m
cord	1.80 m
leather	0.39 m

The lariat was idealized by Adolpho Lutz.

A special supporting team is designated to succour during critical situations caused by an excessive, not foreseen elevation of the water level, or when there is an exceptional agglomeration of animals.

The planning includes rigorous training of the personnel:

1 — *General training* for the personnel, in particular the boat and vehicle crews, consisting of theoretical instructions as to distinction of mammals, reptiles and venomous arthropods of the region; practical courses for the handling of the equipment as lariats, hooks, small and large net-bags, and contention cages, with the use of live animals, preferably snakes, spiders and scorpions supplied by the Instituto Butantan, with posterior evaluation and selection of the individuals more apt for this dangerous type of work.

Physicians of the Instituto Butantan and CESP gave instructions related to first aid, and indication of the sites appointed for specialized treatment of the accidented individuals.

Specialized training

Part of the physicians indicated or invited by CESP, received updating instructions — Venomous animals at the Instituto Butantan, and its hospital "Vital Brazil", specialized in the treatment of individuals accidented by venomous animals. Other physicians received similar instructions at the very hydroelectric headquarters.

Graduated personnel of CESP as biologists, agronomists, forestal engineers, designated to participate in the "Água Vermelha" operation, received courses in basical knowledge referent to venomous animals, and also a course at the ZOO for the recognition of animal species eventually existing in the area of inundation.

The ZOO provided anesthetic guns at the site during the whole rescue operation.

CESP supplied six motorboats, 12 vehicles, and 6 ambulances, two airplanes, and two helicopters to be used in the inundation area; the military police placed at disposal two motorboats and maintained the whole area under radiocontrol.

The boats and vehicles were equipped with hatchets, leather gloves — medium length, helmets, snares and hooks on a 1.50 m long handle, ropes, burlap sacs to transport mammals and reptiles, boxes, 40 cm screw driver, spare screws, life belts; leather boots or half boots for the occupants of the vehicles were provided.

The Medical Department of CESP acquired the following types of antivenins to be distributed according to the planning norms: At the base station — CESP Hospital in Indaiaporã — 100 ampoules of antiophidic serum, 30 amp. antielapidic serum, and 30 amp. antiarachnidic serum. The other stations received 40 amp. antiophidic serum, and 5 antielapidic serum each.

In the N.^o 2 region, a closed shelter was provided, with electricity, piped water and sewer, for the recuperation of animals affected by the flood and by capture.



With regard to the preservation of the local fauna, CESP selected (through Ladislau A. Deutsch, biologist of the ZOO) and acquired an area of approximately 145.2 ha, 46.8 ha of which predominantly secondary woodland, situated in Paulo de Faria as a biological refuge.

Accomplishment and Results

The floodgates were closed on 26-6-78, and the water level rose until 11-8-78. At the start of the damming, the water level was of 341.26 m, and attained a stable level at the 376.57 m quota. The water rose 35.31 m on the whole. During these 46 days, the main animal rescue took place (Fig. 10). On the first day, the water rose about 6.19 m near the dam, and reached the N.º 1 and 2 region; on the second day, the water rose 2.42 m, on the 3rd, 4th, and 5th day, about 1 m decreasing gradually with some alteration up to the last week, when the variation was less than 0.20 m per day (Fig. 10).

For each region a detailed control chart as to rescue was elaborated, specifying the number of mammals, birds, reptiles, and arachnids (CESP, 1978 c).

During these 46 days, 3263 animals were captured (CESP, 1978 c), 1608 of which mammals (49,279%), 1621 reptiles (49,678% — 1530 snakes, 5 alligators, 86 lizards), 18 arthropods (0,551%), and 16 birds (0,490%).

Mammals

- 830 — *Callithrix jacchus penicillata* (Hershkovitz, 1968)
- 197 — *Cebus* sp. (Linnaeus, 1758)
- 186 — *Coendu prehensilis* (Linnaeus, 1758)
- 166 — *Didelphis aurita* (Wied, 1820)
or *Didelphis marsupialis* (Linnaeus, 1758)
- 132 — *Alouatta caraya* (Humboldt, 1812)
- 16 — *Cavia aperea* (Erxleben, 1777)
- 16 — *Rattus* sp.
- 9 — *Tamandua tetradactyla* (Linnaeus, 1758)
- 8 — *Lepus* sp.
- 4 — *Euphractus sexcinctus* (Linnaeus, 1758)
- 3 — *Dasybus novemcinctus* (Linnaeus, 1758)
- 2 — *Myrmecophaga tridactyla* (Linnaeus, 1758)
- 2 — *Nasua nasua* (Linnaeus, 1758)
- 1 — *Ozotoceros bezoarticus* (Linnaeus, 1758)

Domestic animals

- 30 — cats
- 5 — bovines
- 1 — dog

Birds did not present much trouble, even so 16 specimens needed the help of the rescue team. Loss of nests and young naturally had to be considered.

Of a total of 3263 captured animals in "Água Vermelha", 1621 reptiles (49,678%) predominated with the following distribution: 1530 ophidians (46,889%), 86 lizards (2,635%), and 5 alligators (0,153%).



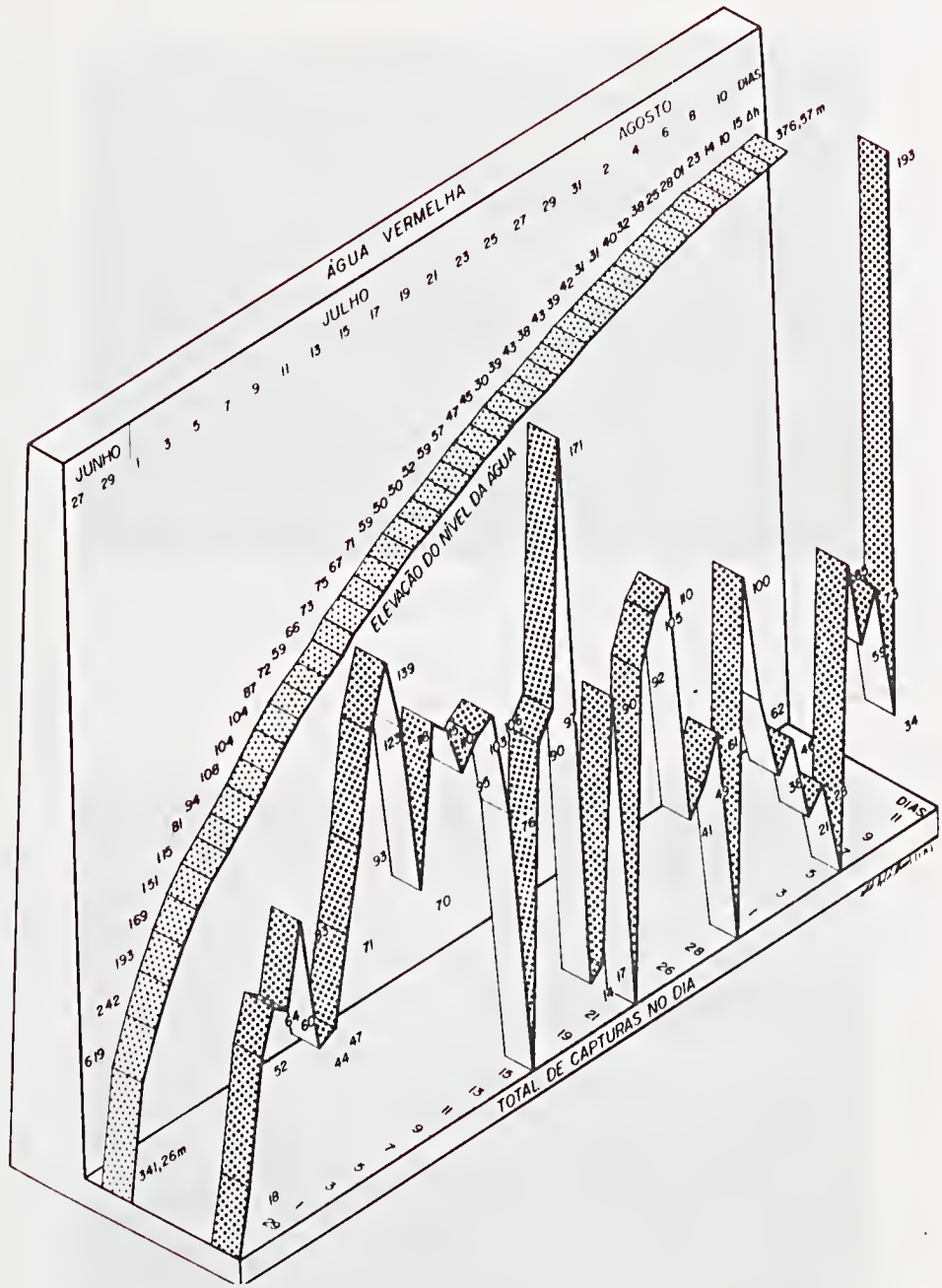


Fig. 10 — Daily capture of animals, during the rising of the water level, from June 27th to August 10th, 1978.



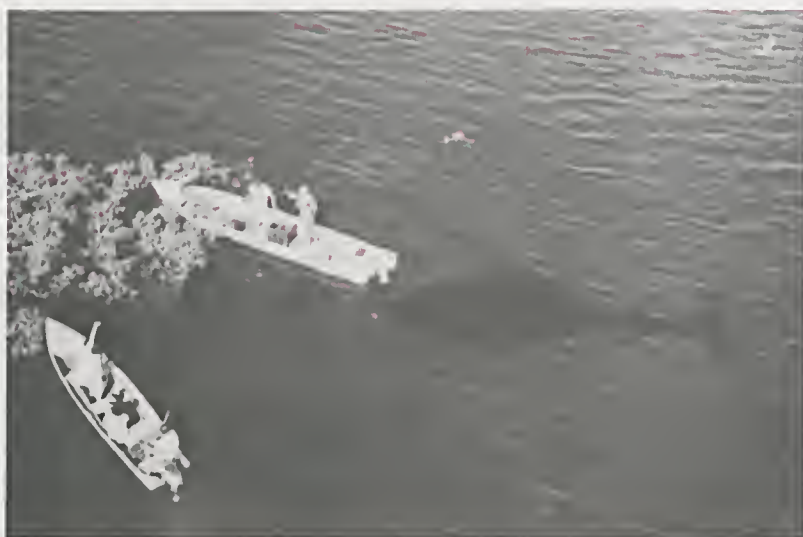


Fig. 11 — Photo Giuseppe Puerto — Boats and helicopter in action.



Fig. 12 — Photo Giuseppe Puerto — Part of the impoundment area.

REPTILIA: SERPENTES

ANOMALEPIDIDAE

- 4 — *Typhlops squamosus* (Schlegel, 1839)

BOIDAE

- 94 — *Boa constrictor amarali* (Stull, 1932)
23 — *Epicrates cenchria crassus* Cope, 1862
7 — *Eunectes murinus scytale* (Linnaeus, 1758)

COLUBRIDAE

- 2 — *Apostolepis assimilis* (Reinhardt, 1861)
1 — *Chironius bicarinatus* (Wied, 1820)
21 — *Chironius flavolineatus* (Boettger, 1885)
38 — *Chironius quadricarinatus* (Boie, 1827)
5 — *Clelia occipitolutea* (Duméril, Bibron e Duméril, 1854)
29 — *Leimadophis almadensis* Wagler, 1824
— *Leimadophis poecilogyrus schottii* (Schlegel, 1837)
— *Leimadophis maculicauda* Amaral, 1927
40 — *Drymarcon corais corais* (Boie, 1827)
1 — *Elapomorphus nasutus* Gomes, 1915
2 — *Erythrolampus aesculapii vcnustissimus* Wied, 1821
4 — *Helicops carinicaudus infrataeniatus* (Jan, 1865)
4 — *Helicops modestus* Guenther, 1861
3 — *Hydrodynastes bicinctus schultzi* Hoge, 1966
19 — *Hydrodynastes gigas* (Duméril, Bibron e Duméril, 1854)
10 — *Leptodeira annulata annulata* (Linnaeus, 1758)
7 — *Liophis brazili* (Amaral, 1923)
6 — *Liophis jaegeri* (Guenther, 1858)
2 — *Liophis occipitalis* (Jan, 1863)
4 — *Lygophis flavifrenatus* Cope, 1862
4 — *Lygophis meridionalis* (Schenkel, 1901)
34 — *Mastigodryas bifossatus bifossatus* (Raddi, 1823)
2 — *Oxyrhopus petola digitalis* (Reuss, 1834)
9 — *Oxyrhopus trigeminus gubei* (Duméril, Bibron e Duméril, 1854)
72 — *Philodryas olfersii* (Lichtenstein, 1823)
2 — *Philodryas patagoniensis* (Girard, 1857)
2 — *Pseudoboa nigra* (Duméril, Bibron e Duméril, 1854)
2 — *Rachidclus brazili* Boulenger, 1908
3 — *Simophis rhinostoma* (Schlegel, 1837)
1 — *Spilotes pullatus pullatus* (Linnaeus, 1758)
33 — *Thamnodynastes nattereri* (Mikan, 1828)
3 — *Waglerophis mcrrerii* (Wagler, 1824)
1 — *Sibynomorphus mikanii mikanii* (Schlegel, 1887)

ELAPIDAE

- 1 — *Micrurus lemniscatus carvalhoi* (Roze, 1967)
1 — *Micrurus frontalis braziliensis* (Roze, 1967)

VIPERIDAE

- 46 — *Crotalus durissus collilineatus* Amaral, 1926
— *Crotalus durissus terrificus* (Laurenti, 1768)
7 — *Bothrops alternatus* (Duméril, Bibron & Duméril, 1854)
554 — *Bothrops moojeni* Hoge, 1966
2 — *Bothrops neuwiedi pauloensis* Amaral, 1925

The venomous ophidians (611), and part of the non venomous (404), after prior identification, were sent to the Instituto Butantan for venom extraction, and to constitute the sampling material of the area respectively; the remainder of the non venomous ophidians (515), as well as 181 specimens of *Boa constrictor amarali*, 47 *Drymarcon corais corais*, the 7 specimens of *Eunectes murinus*, and others were released in areas adjacent to the sites of capture or in the faunal refuge of "Paulo de Faria".

LACERTILIA

TEIIDAE

- 71 — *Tupinambis teguixin* (Linnaeus, 1758)

GEKKONIDAE

- 8 — *Hemidactylus* sp. Gray, 1825

AMPHISBAENIDAE

- 7 — *Amphisbaena* sp. (Linnaeus, 1758)

CROCODILIA

- 5 — *Caiman latirostris* (Daudin, 1802)

ARANEAE

THERAPHOSIDAE

- 6 — *Acanthoscurria* sp.

- 5 — *Pamphobeteus* sp.

PISAUROIDAE

- 2 — *Ancylometes* sp.

CTENIDAE

- 1 — *Phoneutria* sp.

EUSPARASSIDAE

- 1 — *Polybetes* sp.

During the first phase of inundation, the rescued animals were released in regions of previously selected forests. Those animals rescued during the second phase, were taken to the faunistic refuge of "Paulo de Faria", acquired in the meantime by CESP.

At an advanced phase of the operation, the autonomous regions N.º 5 and 6 were incorporated into N.º 3 and 4 respectively, at the extreme end of the dam, from 02/07/78 onwards.

The general Coordination Department of CESP, entrusted its functionary Pedro Castelo Branco Rosário with the execution of the rescue operation (CESP, 1978 *c*); he preferred to use the buildings in Indiaporã as headquarters, geographically much more appropriate, instead of Cardoso, initially designated for the later inundation phase.

The rescue operation was terminated on 11/08/78, even so a single team continued to inspect by boat and by plane the areas in search of lost animals.

During this complementary phase the whole area was seemingly cleared.

In conformity with the prevision related to ophidic accidents, only one case, probably *Bothrops*, was confirmed in the Mira Estrela municipality; the individual was treated in the CESP Hospital, and recovered within three days (CESP, 1978 *c*).

The execution of the rescue operation under the total responsibility of CESP, upstream of "Água Vermelha", concerning mammals, reptiles, birds, and arthropods involved 20 selected employees of CESP, 8 of the ZOO-BUTANTAN team, 12 militaries of the Minas Gerais State, 47 militaries of the São Paulo State (the latter working in shifts), four students of the Faculty of Veterinarian Medicine from the University of São Paulo, one journalist of the "Secretaria da Saúde" of the São Paulo State, 6 physicians of CESP or invited to participate, 6 male nurses besides biologic specialists, forestal engineers, agronomists of the Department of Natural Resources of CESP, who assisted in the project, and were in charge of the ichthyological rescue downstream of the dam. The rescue operation was once more nicknamed "Ark of Noah".

The cinematographic, photographic, and journalistic documentation was the responsibility of the Public Relation Department of CESP, with the collaboration of specialized technicians of the "Secretaria da Saúde" and the ZOO.

DISCUSSION AND CONCLUSIONS

Analysing and comparing the anticipated planning results in "Água Vermelha" with those obtained during prior operations at other reservoirs accomplished by Belluomini, Cembranelli, and Autuori (1976/7), it became evident that intensive training, and selection of apt personnel constitute fundamental prerequisites.

Critical aspects of faunal rescue, that began with delay in areas of great barrages, are reported by Critchley (1959), Harthorn and Lock (1960), and Walsh & Gannon (1967).

In an attempt to maintain the biological equilibrium rodent-snake, according to Walsh and Gannon, non venomous snakes, mainly *Boa constrictor amarali* were returned to their natural habitat.

Topographic survey, to determine the regions to be deforested, confirmation of the presence of animals, and the preparation of migratory routes to pre-selected habitats, are necessary to warrant a favorable development of the rescue operation.

The prevalence of ciliary forests in "Água Vermelha" involved a higher agglomeration of mammals, mainly monkeys and hedgehogs, generally captured with difficulty, and required frequently awaiting of the rise of water with consequent flight of the animals to the top of the trees, whose branches often had to be cut, bringing the animals down to the water, thus facilitating capture. This alternative may cause exhaustion, discomfort and hunger to them.

The rescue of animals in non deforested areas was slower and demanded more attention from the boat crews, due to the risk represented by carnivorous ants, wasp nests, hornets, and the encounter with venomous snakes.

Groups of delayed animals composed of females, males and young, required more intense pursuit.

Drowning of some animals of subterraneous habits is inevitable, considering the extension of the areas to be searched, and the speed of the rising waters.

The practical knowledge acquired through each new salvage operation, always improving the methodology employed as yet, grants a gradual elimination of eventual faults in future work.

The cultivated areas, mainly those with grain crops, bring forth an elevated populational density of rodents, and a consequent presence of mainly venomous ophidians, in search of their favorite food (Belluomini, 1968).

The presence of *Bothrops moojeni* (a very large venomous snake, quick and dangerous, inclusive at capturing), commonly called "caïçaca" or improperly "jararaca", was confirmed in the N.º 1 region by the capture of 266 specimens; in N.º 2 by 167, followed by 49 and 72 specimens respectively in N.º 3 and N.º 4 regions, surpassing any expectation.

In these regions were captured also part of the 46 specimens of *Crotalus durissus terrificus*, and *C. durissus collilineatus* commonly denominated rattlesnake, whose bite is the most feared (Rosenfeld, 1971) due to the high death rate in humans and animals. There were also captured 7 *Bothrops alternatus*, 2 *B. neuwiedi pauloensis*, and 2 true coral snakes, *Micrurus lemniscatus carvalhoi* and *M. frontalis braziliensis*.

Of a total of 3263 animals captured in "Água Vermelha", 1621 reptiles (49.678%) predominated in the following distribution: 1530 ophidians (46.889%), 86 lizards (2.653%), and 5 alligators (0.153%).

Among the 1530 snakes, 611 were venomous (39.934%) representing 18.725% of the total rescued animals, transforming the operation "Água Vermelha", among those coordinated by the ZOO-BUTANTAN team, the most dangerous ever accomplished. After the conclusion of the rescue operation, no animals could be found any more (CESP, 1978 c).

The faunistic refuge acquired by CESP in "Paulo de Faria" (at the left border of the reservoir) is being controlled and closely observed.

An agreement between "Furnas Centrais Elétricas" and the "Universidade Federal de Minas Gerais" (UFMG) facilitated the studies related to the planning in "Itumbiara" in 1979.

On the day when the studies in their entirety composed by local ecological and faunal survey, as well as anticipated planning — deforesting and preparation of special migration routes, selection of a faunal refuge, training of personnel — becomes concordant with the consequent inexpressive capture of animals, the real objective of the enterprise shall be attained.

The protection of nature needs more and more actuating individuals endeavoured in the preservation of the ecological patrimony.

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OFÍDIOS DA AMAZÔNIA

XV — AS ESPÉCIES DE *CHIRONIUS* DA AMAZÔNIA ORIENTAL (PARÁ, AMAPÁ E MARANHÃO). (OPHIDIA: COLUBRIDAE)

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Francisco Paiva do NASCIMENTO *

RESUMO: Em grande parte do Brasil e particularmente na região Amazônica, as espécies de *Chironius* são pouco conhecidas e imperfeitamente estudadas. Para tal, reuniu-se 379 exemplares do gênero em questão, para uma reavaliação das espécies que ocorrem na região oriental da Amazônia, abrangendo os Estados do Pará e Maranhão e o Território Federal do Amapá. São redefinidas através de análise comparativa e confrontadas com os dados da literatura. Neste trabalho são válidas as seguintes espécies: *Chironius carinatus*, *C. exoletus*, *C. scurrulus*, *C. fuscus* (forma até então confundida com *Natrix cinnamomea* Wagler), *C. multiventris* (forma antes identificada como *C. cochranæ* Hoge & Romano) e por fim a primeira citação da ocorrência na Amazônia da espécie *C. flavolineatus*, dos cerrados do leste e centro do Brasil, até Mato Grosso e Paraguai.

INTRODUÇÃO

O gênero *Chironius* ocorre em quase toda a América do Sul, sendo porém pouco conhecidas as suas espécies, porque algumas delas têm permanecido mal definidas sob o ponto de vista taxonômico. Desde quando Boulenger (1894:71) englobou sob a denominação de *Herpetodryas* Boie, 1826, cinco espécies que considerou típicas e colocou na sinonímia destas, outras até então descritas, deste status surgiu muita confusão posterior.

Amaral (1930:160) adotando em parte a proposição de Boulenger, simplificou mais ainda o número de espécies para três, sinonimizando algumas designações sob *Coluber carinatus* Linnaeus, 1758 (= *Chironius carinatus*) e *Coluber fuscus* Linnaeus, 1758 (= *Chironius fuscus*). Sugeriu ainda uma revisão do gênero, que até hoje não foi levada a cabo no conjunto geral.

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Bailey (1955) tentou sistematizar as *Chironius* do sudeste da América do Sul, em particular as do leste do Brasil, e as do Paraguai e Argentina. Neste trabalho o autor estabeleceu padrões morfológicos para definir sete espécies, das quais uma foi descrita como nova (*C. foveatus*), três descritas por Wied, então revalidadas (*C. bicarinatus*, *C. pyrrhopogon* e *C. laevicollis*), uma de Linnaeus (*C. fuscus*), uma de Boettger (*C. flavolineatus*) e uma de Boie (*C. quadricarinatus*), e por fim determinando aproximadamente a distribuição geográfica e ocorrências das mesmas.

A chave elaborada pelo autor para identificar estas *Chironius*, bem como as tabelas dos caracteres merísticos (folidose dorsal e anal, dentes maxilares, escamas ventrais e escudos cefálicos), são claros e de grande utilidade para o melhor conhecimento das espécies deste gênero.

Donoso-Barros (1969:189) quis também contribuir com alguns dados, arranjando uma chave geral das espécies então admitidas (cerca de vinte), ao mesmo tempo que tirava do esquecimento *Herpetodryas holochlorus* Cope, 1876, *Coluber spixii* Hallowell, 1845 e descrevia uma espécie nova *C. barrioi*. A chave apresentada pelo autor parece deixar dúvidas pois além de superficial, não analisa a identidade das espécies e por isso não a tomamos como fundamental. Quase simultaneamente, Peters & Orejas-Miranda (1970:58) na chave para *Chironius*, consideraram 16 designações para a região Neotropical, em parte baseado no trabalho de Bailey (1955).

Pelo exposto, constatamos que na área Amazônica, as espécies de *Chironius* estavam e em parte ainda permanecem pouco conhecidas e estudadas, por ora na parte ocidental dessa região, devido principalmente à pobreza de exemplares em coleções. A Seção de Herpetologia do Museu Paraense nestes últimos 15 anos vem tentando sanar o problema de coleções herpetológicas deficientes, através de capturas maciças de ofídios, em particular nas áreas do Pará, Amapá e Maranhão. Assim foi possível contar com abundante material para podermos elaborar o presente trabalho sobre as espécies de *Chironius* de uma parte da Amazônia, contribuindo deste modo para o conhecimento mais seguro do gênero e servir para uma futura revisão do mesmo.

MATERIAL E MÉTODOS

Foram estudados 379 exemplares, entre jovens e adultos assim distribuídos por espécie:

Chironius carinatus (fig. 1)

38 exemplares — 25 ♂, 11 ♀.

Chironius exoletus (fig. 2)

157 exemplares — 69 ♂, 88 ♀.

Chironius flavolineatus (fig. 3)

2 exemplares — 1 ♂, 1 ♀.

Chironius fuscus (fig. 4)

77 exemplares — 40 ♂, 37 ♀.

Chironius multiventris (figs. 5 e 6)

76 exemplares — 48 ♂, 28 ♀.

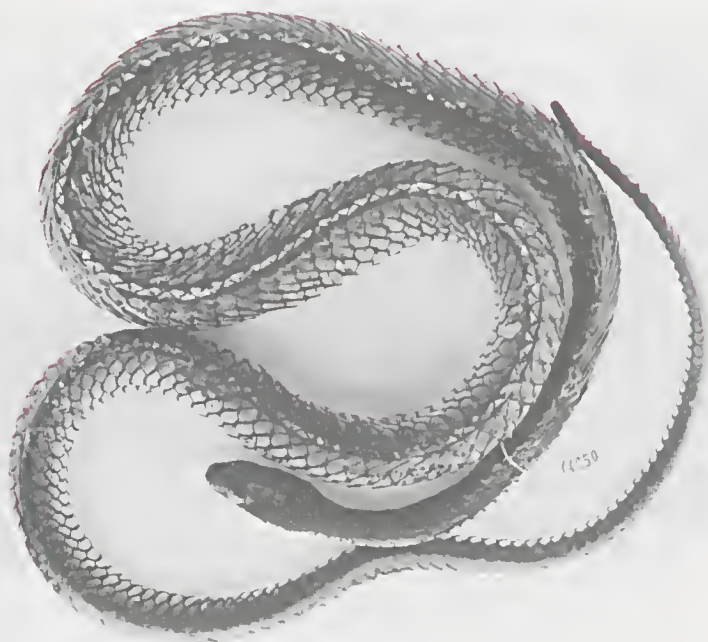


Fig. 1 — *Chironius carinatus* ♂



Fig. 2 — *Chironius exoletus* ♂



Fig. 3 — *Chironius flavolineatus* ♂

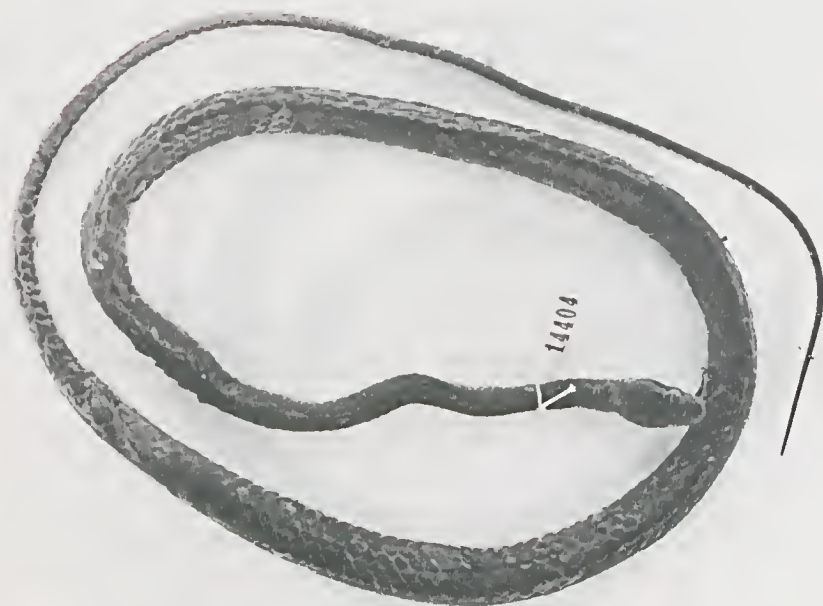


Fig. 4 — *Chironius fuscus* ♀

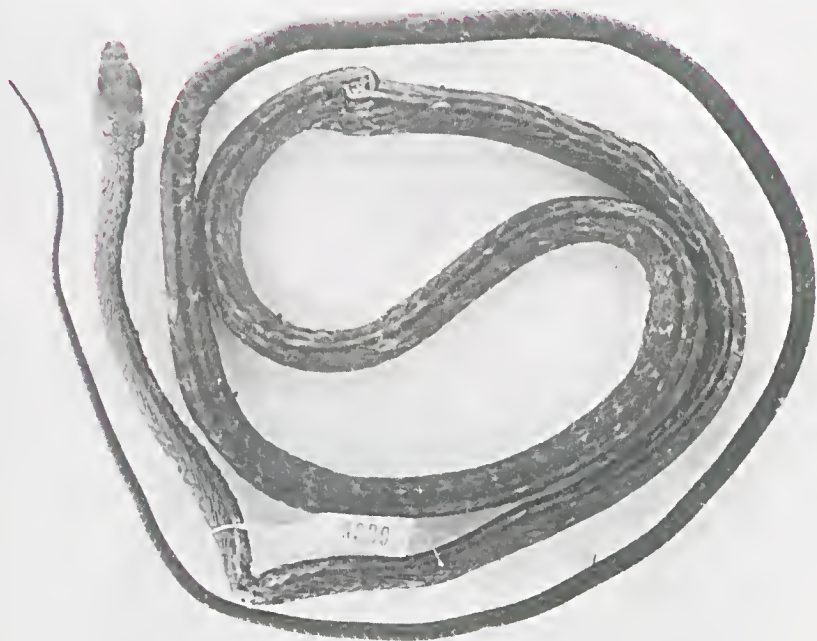


Fig. 5 — *Chironius multiventris* ♂



Fig. 6 — *Chironius multiventris* ♀

Chironius scurrulus (fig. 7)

29 exemplares — 19 ♂, 10 ♀.

Todos os exemplares acham-se conservados na Seção de Herpetologia do Museu Paraense Emilio Goeldi. A análise dos caracteres está assinalada nas respectivas tabelas aqui incluídas. A totalidade dos espécimes estudados procede do Estado do Pará, Maranhão e Território do Amapá. Para comparação e complementação das análises foram incluídos alguns indivíduos coletados no Estado do Amazonas, norte de Mato Grosso (Rio Aripuanã, Cachoeira Dardanelos) e Território de Roraima.



Fig. 7 — *Chironius scurrulus* ♂

O presente trabalho não pretende constituir uma revisão, mesmo parcial, do gênero *Chironius*, mas apenas definir as espécies que ocorrem em uma ampla área da Amazônia, onde as mesmas permaneciam imperfeitamente caracterizadas. Foram considerados os seguintes principais caracteres específicos, conforme o padrão estabelecido por Bailey (1955): variação das escamas dorsais; pré e postoculares; temporais; supra e infralabiais (incluindo os que tocam na órbita e os que contactam com os mentais anteriores); fossetas apicais das escamas; ventrais; anal inteira ou dividida; caudais; dentes maxilares; colorido padrão e suas variantes; e dimorfismo sexual.

Apesar destas análises, continuam ainda certas dúvidas de ordem taxonômica, tais como a validade de várias designações específicas e a possível ocorrência de subespeciação para algumas formas mal conhecidas, que ocorrem em extensas áreas. Somente uma revisão geral do gênero, fundamentada em abundante material, abrangendo várias críticas da América do Sul, poderá determinar a real situação das espécies ou raças que compõem o gênero *Chironius*.

Conforme os dados por nós obtidos e confrontados com os encontrados na literatura mais recente foi possível confirmar a ocorrência de 6 espécies para a região oriental da Amazônia. Destas, ratificamos a forma *C. exoletus* (Linnaeus), recentemente revalidada por Hoge, Romano & Cordeiro (1976/77:41), encontrada no Maranhão, mas que agora sabemos ser uma espécie comum na Amazônia; *C. cinnamomeus* considerada por Hoge (1964:53) e Cunha & Nascimento (1978:62), agora passa com toda certeza a ser sinônima de *C. fuscus* (Linnaeus), largamente caracterizada pelos mais recentes autores como Roze (1966:97); Donoso-Barros (1969:189); Peters & Orejas-Miranda (1970:58) e Dixon & Soini (1977:39); *C. cochranae* Hoge & Romano deve ser admitida como sinônima de *C. multiventris* Schmidt & Walker, pois nós, estudando 76 exemplares, de várias procedências, não nos foi possível diferenciar os caracteres apresentados para uma e outra, nem de ordem geográfica; confirma-se aqui a existência da espécie *C. scurrulus* (Wagler), forma também examinada por Hoge & Nina (1964:72) e já atestada por Dixon & Soini (1977:41), Cunha & Nascimento (1978:64) e Gasc & Rodrigues (1980:572); pela primeira vez identifica-se para a Amazônia a ocorrência de *C. flavolineatus* (Boettger), por sinal uma espécie pouco conhecida, pois foi bem recente revalidada por Bailey (1955:13), esquecida desde a descrição original; por fim define-se a ocorrência de *C. carinatus* (Linnaeus) por muito tempo identificada como *C. exoletus*, *C. bicarinatus*, *C. flavolineatus* e *C. multiventris*. Esta última foi assinalada por Gomes (1918b:66) em 4 indivíduos, porém incluída como *carinatus*.

Família Colubridae
Gênero *Chironius* Fitzinger

Chironius Fitzinger, 1826:31. Espécie tipo: *Coluber carinatus* Linnaeus, 1758.

Diagnose: Cabeça alongada distinta do pescoço; rostral mais alto que largo; focinho obtuso; olhos grandes com pupila redonda. Dois internasais, dois prefrontais, um frontal e dois parietais, um nasal, um loreal, um preocular (raramente dois) e dois postoculares (algumas vezes três), temporais variando de 1 + 1 ou 1 + 2 (raramente 1 + 3 ou 1 + 4). Dentes maxilares 26 a 46, menores adiante e gradualmente aumentados posteriormente, sem diastema ou par de dentes grandes acanalados. Supralabiais 8 a 11 (normalmente 9); infralabiais 9 a 11 (raramente 8 a 12, normalmente 10).

Corpo alongado, comprimido ou não; cauda longa, afilada. Escamas dorsais grandes, carenadas ou lisas, com fossetas apicais, arrançadas obliquamente em grande parte do corpo, em 10 ou 12 filas no meio do corpo, com redução. Ventrals arredondadas ou obtusamente anguladas nos lados, de 139 a 193; anal inteira ou dividida; caudais em 110 a 206, divididas.

Colorido variável, desde o esverdeado, azeitonado ou pardo avermelhado na parte superior e lateral da cabeça e no corpo, ora mais ora menos escurecido, com uma faixa clara vertebral, às vezes acentuada (cor amarela), ora gradualmente indistinta na maior parte das espécies; presença ou não de barras laterais transversais claras.

A diagnose acima está fundamentada quase que exclusivamente nos caracteres apresentados nas espécies que ocorrem na região oriental da Amazônia estudadas neste trabalho.

Chave para as espécies da Amazônia oriental

- | | |
|------------------------------------------------------------------------------------------------------------|----------------------|
| 1 — 10 filas de escamas no meio do corpo | 2 |
| 12 filas de escamas no meio do corpo | 4 |
| 2 — Placa anal inteira | 3 |
| 3 — Dentes maxilares 34 a 37, temporais normalmente 1 + 1; escamas ventrais 150-159, caudais 110-126 | <i>scurrulus</i> |
| Dentes maxilares 42 a 46, temporais normalmente 1 + 1; escamas ventrais 140-154, caudais, 115-130 | <i>fuscus</i> |
| 4 — Placa anal dividida | 5 |
| 5 — Menos de 180 escamas ventrais e menos de 180 caudais | 6 |
| Acima de 180 ventrais e mais de 180 caudais | 9 |
| 6 — Dentes maxilares menos de 30 | 7 |
| Dentes maxilares acima de 30 | 8 |
| 7 — Temporais 1 + 2; ventrais 139-160 e caudais 120-148, dentes maxilares 26 a 30 | <i>exoletus</i> |
| 8 — Supralabiais 8; dentes maxilares 30 a 35; ventrais 150-162, caudais 116-133 | <i>carinatus</i> |
| Supralabiais 9; dentes maxilares 33 a 41; ventrais 151-154, caudais 140 | <i>flavolineatus</i> |
| 9 — Dentes maxilares 34 a 38; 1 pré e 3 postoculares em geral; ventrais 183-193, caudais 189-201 | <i>multiventris</i> |

Chironius scurrulus (Wagler)

Natrix scurrula Wagler, 1824, 24. pl. 8. Localidade típica: Rio Japurá, Estado do Amazonas.

Herpetodryas fuscus; Boulenger, 1894. [partim], 2:75 [tipo E]; Gomes 1918a:509; Gomes, 1918b [partim] 64.

Chironius scurrulus Hoge & Nina, 1964:72; Dixon & Soini, 1977:41; Cunha & Nascimento, 1978:64.

Diagnose — Nasal dividido; loreal mais longo que largo; órbita com diâmetro maior que sua distância da narina; 1 pré e 2 postoculares (raramente 3); temporais 1 + 1 (raramente 1 + 2); supralabiais 9-9 usualmente (muito raro 10-10), 4.^o, 5.^o e 6.^o normalmente tocando a órbita, às vezes 5.^o e 6.^o ou 5.^o, 6.^o e 7.^o; infralabiais 11-11 ou 10-10 usualmente, às vezes 10-11 e raramente 9-10 (com tendência para 6 em contato com o mental anterior ou também 5, às vezes 5-6); mentais anteriores mais curtos que os posteriores. Escamas dorsais normalmente em 10-10-10 séries longitudinais (raramente 10-10-8, 10-10-9 e 11-10-10),

todas lisas, sem filas de carenas vertebrais; escamas laterais oblíquas, com fossetas apiculares presentes (normalmente uma, muito raro duas) na região nugal e pescoço ou um pouco mais, ausentes na região anal. Anal inteira. Dentes maxilares 34-37. Ventrais, machos, 150 a 158; fêmeas 150 a 159; caudais divididas, machos 111 a 126 e fêmeas 110 a 115. Comprimento encontrado nos espécimes n.º 13.554 — Paruá (Maranhão), 1.205 mm de corpo e 613 mm de cauda (total 1.818 mm); n.º 425, rio Tracajatuba (reserva do DNERu-Amapá), 1.445 mm de corpo e 291 mm de cauda com mais da metade partida (total 1.736 mm).

Colorido em preservativo: Dorso pardo claro, às vezes escuro, com escamas ora mais ora menos pigmentadas de pardo ou negro, irregularmente dispostas; cabeça mais escura que o corpo; ventre amarelado com ou sem manchas escuras na parte lateral. A parte anterior do corpo (pescoço) de aspecto mais escurecido.

Comentários — Boulenger (1894:75) sinonimizara *Natrix scurrula* Wagler na espécie *Herpetodryas fuscus* (Linnaeus) (= *Chironius fuscus*), embora tivesse feito ressalva em separado, para dois indivíduos do Peru, quanto ao aspecto do colorido (tipo E). Assim, aquele autor considerara os caracteres de *C. fuscus* demasiadamente amplos, sem levar em conta, pelo menos, mais dois importantes aspectos que separam ambas formas: a denteção do maxilar, elevada em *fuscus* e a ausência de carenas vertebrais em *scurrulus*.

Desta época em diante a espécie *scurrulus* deixará de aparecer na referência dos especialistas até que Hoge & Nina (1964:72) resolveram revalidar a espécie descrita por Wagler em 1824. Antes porém Gomes (1918b:64) referiu dois exemplares do Pará (n.º 24 e 25) que parecem identificar-se a *C. scurrulus*, pelos caracteres de coloração e ventrais mais altas que o normal encontrado em *C. fuscus*. Ainda o mesmo Gomes (1918a:509), ao estudar os ofídios do Museu Rocha, de Fortaleza, citou um exemplar do Amazonas com as características de *scurrula* de Wagler, indicado pelo próprio autor.

Hoge & Nina (1964:72) apresentaram uma satisfatória redescritção de *Chironius scurrulus*, que vem servindo de padrão para a identificação da espécie. A mesma apresenta atualmente, conforme trabalhos recentes, uma ampla distribuição no Brasil (Amazonas, Pará, Amapá, Rondônia, Minas Gerais, Maranhão e talvez outros Estados); Guiana Francesa segundo Gasc & Rodrigues (1980:572); Peru de acordo com Dixon & Soini (1977:41), para a região de Iquitos, cujos dados ajustam-se aos exemplares estudados no presente trabalho e Colômbia segundo citação de Peters & Orejas-Miranda (1970:61).

Foram examinados 29 exemplares, dos quais 19 machos e 10 fêmeas. O diformismo sexual é pouco perceptível nas escamas ventrais, porém diferindo nas caudais; aquelas quase idênticas nos dois sexos, enquanto nestas as fêmeas as possuem acentuadamente em menor número.

A espécie é pouco freqüente, em relação às outras espécies de *Chironius*. Tem sido encontrada em mata primária, capoeiras, roçados, várzeas e possivelmente cerrados. Alimenta-se preferentemente de Anfíbios (rãs, *Hyla*, *Leptodactylus* e talvez *Eleutherodactylus*) conforme atesta a análise do conteúdo estomacal.

Material examinado: verificar tabela anexa.

TABELA 1
Chironius scurrulus — Amapá

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infrac. Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anel	Coletor
424	Reserva Onere Rio Tracajuba	08/09	♂	10-10-10	151	1	—	9/9	10/10	42.7	1.003	—	—	1+2	1+1	—	Nascimento
425	Reserva Onere Rio Tracajuba	08/09	♀	10-10-10	155	1	—	9/9	10/11	54.0	1.445	—	—	1+2	1+1	—	Nascimento
Chironius scurrulus — Maranhão																	
12.248	Nova Vida	06/76	♂	10-10-10	150	1	117/118	9/9	10/10	17.5	798	400	—	1+2	1+1	—	Cunha & Nascimento
12.297	Pará	10/78	♂	10-10-10	155	1	112/112	9/9	10/10	34.5	803	387	—	1+2	1+1	—	Nascimento
13.554	Pará	10/76	♀	10-10-10	156	1	115/115	10/10	11/11	50.0	1.205	613	—	1+2	1+1	—	Nascimento
Chironius scurrulus — Pará																	
239	Santa Bárbara	05/64	♂	10-10-9	150	1	—	9/9	10/10	13.0	283	—	—	1+2	1+1	—	Moreira
357	APEG — Belém	1969	♂	10-10-10	153	1	—	9/9	11/11	49.0	1.125	—	—	1+2	1+1	—	—
975	Boa Vista	11/71	♂	10-10-10	150	1	110/113	9/9	11/11	17.7	305	145	—	1+2	1+1	—	Cunha & Nascimento
991	Boa Vista	11/71	♀	10-10-10	155	1	—	9/9	11/11	58.0	1.400	—	—	1+2	1+1	—	Cunha & Nascimento
1.166	Boa Vista	08/72	♂	10-10-10	153	1	117/117	9/9	11/11	17.4	310	147	—	1+2	1+1	—	Cunha & Nascimento
1.168	Boa Vista	08/72	♀	11-10-10	153	1	115/115	9/9	11/10	17.0	305	149	—	1+2	1+1	—	Cunha & Nascimento
4.768	Boa Vista	10/73	♀	10-10-10	153	1	—	9/9	10/10	61.5	1.375	—	—	1+2	1+1	—	Cunha & Nascimento
5.172	Colônia Nova	10/73	♂	10-10-10	153	1	117/117	9/9	11/11	17.0	325	148	—	1+2	1+1	—	Cunha & Nascimento
5.764	Bom Jesus	09/74	♂	10-10-10	154	1	117/117	9/9	11/11	43.0	950	510	—	1+2	1+1	—	Cunha & Nascimento
6.130	Km 74 da BR-316	09/74	♂	10-10-10	151	1	—	9/9	11/11	44.4	1.010	—	—	1+2	1+1	—	Barata
6.981	Santo Antonio do Tauá	07/74	♀	11-10-10	153	1	111/111	9/9	10/11	39.0	827	450	—	1+2	1+1	—	Cunha & Nascimento
7.460	Km 11 da PA-332	07/74	♂	10-10-8	152	1	111/111	9/9	10/10	39.0	956	473	—	1+2	1+1	—	Cunha & Nascimento
7.661	Boa Vista	10/74	♀	10-10-10	157	1	—	9/9	10/11	35.5	810	—	—	1+2	1+1	—	Cunha & Nascimento
8.586	Boa Vista	02/75	♂	10-10-10	154	1	—	9/9	10/11	48.0	1.367	—	—	1+2	1+1	—	Cunha & Nascimento
Chironius scurrulus — Pará																	
9.311	Santa Rosa — Vigia	06/75	♂	10-10-10	155	1	—	9/9	11/11	40.3	1.040	—	—	1+2	1+1	—	Cunha & Nascimento
9.340	Santa Rosa — Vigia	06/75	♀	10-10-10	159	1	113/113	9/9	11/11	35.6	820	445	—	1+2	1+1	—	Cunha & Rosemire
9.423	Tomb-açú	06/75	♂	10-10-10	150	1	126/126	9/9	10/10	23.0	599	330	—	1+2	1+2	—	Cunha & Rosemire
9.915	Cocal	06/75	♂	10-10-10	150	1	—	9/9	9/10	45.6	1.025	—	—	1+2	1+1	—	Cunha & Rosemire
11.258	Km 11 da PA-332	06/76	♂	10-10-10	158	1	—	9/9	10/11	43.0	959	—	—	1+2	1+1	—	Cunha & Nascimento
12.939	Jarbas Passarinho	06/76	♀	10-10-10	155	1	113/112	9/9	10/10	39.5	1.015	534	—	1+2	1+1	—	Cunha & Nascimento
14.497	PA-332 Sítio Bela Vista	07/78	♀	10-10-10	154	1	110/110	9/9	11/11	43.4	1.002	494	—	1+2	1+1	—	Cunha & Nascimento
15.134	Ela Vista	10/78	♂	10-10-10	157	1	112/112	9/9	10/10	34.4	740	355	—	1+2	1+1	—	Cunha & Nascimento
16.320	Santo Amaro Sertões	10/78	♂	10-10-10	155	1	—	9/9	11/11	45.8	1.065	—	—	1+2	1+1	—	Cunha & Nascimento
16.980	Teófilo Otonari Área da Eucaliptaria	02/81	♂	10-10-10	154	1	—	9/9	10/10	28.0	610	—	—	1+2	1+1	—	Milton Gonçalves

Chironius fuscus (Linnaeus)

Coluber fuscus Linnaeus, 1758:222. Localidade tipo: Ásia (in error)

Herpetodryas fuscus; Boulenger, 1894 [partim]:75; Gomes, 1918b [partim]:64.

Chironius fuscus; Amaral, 1930:161; Bailey, 1955:19; Roze, 1966:97; Peters & Orejas-Miranda, 1970:60; Dixon & Soini, 1977:39.

Chironius cinnamomeus; Cunha & Nascimento, 1978:62.

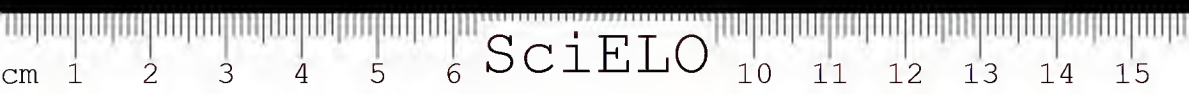
Diagnose — Nasal dividido; loreal mais longa que larga; órbita com diâmetro maior que sua distância da narina; 1 pré e 2 postoculares, raramente 3; temporais 1+1; supralabiais 9-9, raramente 9-10 (4.º, 5.º e 6.º, sempre tocando a órbita); infralabiais 10-10 usualmente, às vezes 10-11, 11-11, 9-9 e 9-10 (5 normalmente em contato com o mental anterior, às vezes 5-6 ou 6); mentais posteriores maiores que os anteriores. Escamas dorsais normalmente em 10-10-10 séries longitudinais (às vezes 10-10-9), com duas filas de escamas carenadas que se estendem até a cloaca ou pouco adiante (muito mais acentuadas nos machos); escamas laterais oblíquas; fossetas apiculares (normalmente 1 em cada escama raramente 2 ou mais raro ainda 3) presentes na nuca, parte do pescoço e raramente na altura da região anal. Anal inteira. Dentes maxilares 42-46. Ventrais, machos 144-154 e fêmeas 142-152; caudais, machos 115-126 e as fêmeas 117-130.

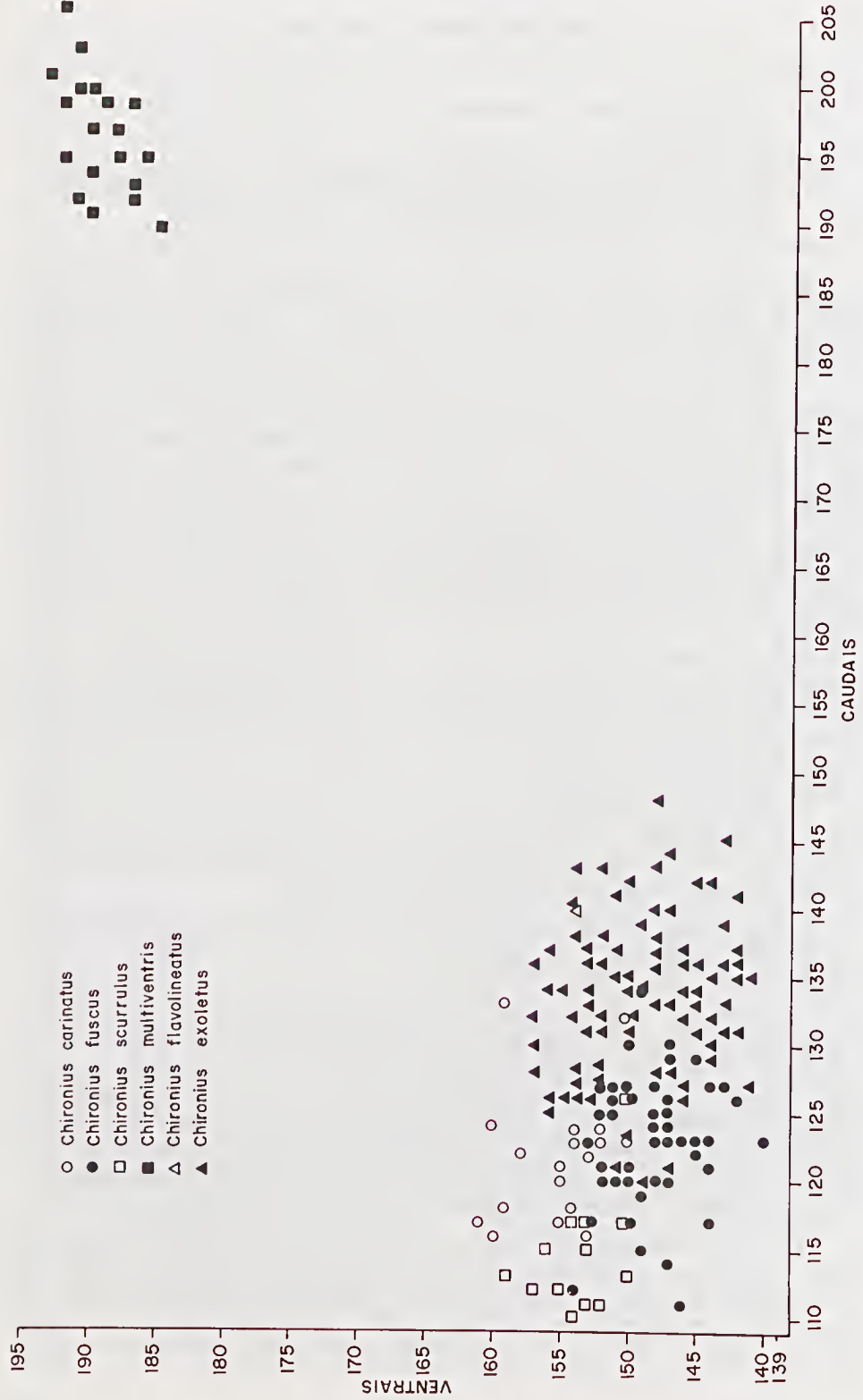
Colorido em preservativo: Dorso e lados pardo, pardo escuro ou pardo azulado; cabeça na parte superior e lados pardo claro até a nuca; uma faixa retro-ocular estende-se até o limite do ângulo da boca; supralabiais esbranquiçadas (possivelmente amarelos em vida) e bem assim os infralabiais, mentais e gulares; região ventral esbranquiçada a amarelo; o tom escuro látero-dorsal estende-se às bordas laterais das ventrais. Cauda idêntica no aspecto do corpo, superior e inferiormente. Em quase todos os exemplares nota-se perfeitamente uma tênue faixa clara vertebral, desde a nuca até quase a região anal, usualmente marginada de um e outro lado por uma tonalidade mais escura.

Comprimento máximo no exemplar n.º 11.156 do lugar Nova Vida BR-316 (25 quilômetros do rio Gurupi), Maranhão, 1.023 mm do corpo e 494 mm da cauda, total 1.517 mm.

Comentários: Esta espécie foi identificada como *C. cinnamomeus* (Wagler, 1824), por Cunha & Nascimento (1978:62), através de dados apresentados por Hoge (1964:53). Porém, estamos certos de que os espécimes coletados no Pará e Maranhão, não podem ser a mesma que Hoge identificara sobre um indivíduo de Suriname como a espécie descrita por Wagler (*Natrix cinnamomea*). O exemplar identificado por Hoge (id.) poderia ser de fato *C. fuscus*, visto os caracteres apresentados coincidirem com os que normalmente vêm sendo atribuídos à esta espécie.

Wagler ao descrever *Natrix cinnamomea* não referiu as escamas dorsais em 10 ou 12 no meio do corpo (por certo, caráter não levado em consideração à época) e nem na região anal, mas acentuou, porém, que o seu exemplar possuía anal inteira, dentes curtos e de mesmo tamanho. Seria o referido indivíduo um representante do gênero *Pseustes*? Boulenger





ger (1894:72) já havia colocado *N. cinnamomea* como sinônimo de *Herpetodryas sexcarinatus* (Wagler, 1824) e hoje sabemos que esta espécie é de fato um representante de *Pseustes*.

Gomes (1918b:64) ao estudar 5 exemplares das coleções do Museu Paraense, todos do Pará, identificou-os como *Herpetodryas fuscus* (Linnaeus) (= *Chironius fuscus*). Os caracteres apresentados em 3 deles (n.ºs 17, 26 e 27) ajustam-se aos espécimes atualmente conservados na Seção de Herpetologia deste Museu e estudados por nós. Gomes cita exemplares de Cametá (Rio Tocantins), Rio Curuá e Rio Iriri, todos com os caracteres seguintes: dorsais em 10, anal dividida, 9 supralabiais (4.º, 5.º e 6.º tocando o olho) e as ventrais 148 a 155 e caudais 116 a 126.

Bailey (1955:19) indicou os caracteres para *C. fuscus* idênticos aos apresentados por Gomes, acima citados, acrescentando mais os dentes maxilares em 41 a 45 e a análise do hemipênis. Aquele autor salientou como caráter distinto a presença de dorsais em 10 no meio do corpo, a anal inteira e os dentes maxilares, os mais elevados entre as espécies de *Chironius*, e bem como os temporais em 1+1.

Dixon & Soini (1977:39) apresentam importantes dados para a melhor caracterização de *C. fuscus*, sobre 54 exemplares do Peru (região de Iquitos). A espécie ocorre em grande parte da América do Sul desde a Venezuela, Guianas, Colômbia, Peru e quase todo o Brasil.

É relativamente freqüente no leste do Pará, porém rara no Maranhão; ocorre ainda em outros locais do Pará, de acordo com tabelas anexas e em Gomes (1918b:65) e no Amapá. Gasc & Rodrigues (1980:572) referiram a ocorrência da espécie na Guiana Francesa, tendo por base 5 exemplares.

Vive em floresta primária, firme e de igapó, capoeiras e roçados. Alimenta-se especialmente de Anfíbios (rãs, possivelmente *Hyla* e *Eleutherodactylus*, conforme atesta a análise do conteúdo estomacal e confirmados também por Dixon & Soini (1977:39).

Material examinado: verificar tabela na pág. 152.

Chironius exoletus (Linnaeus)

[*Coluber*] *exoletus* Linnaeus, 1758:223. Localidade típica.

Indiis (in error).

"*Coluber exoletus*"?, *Herpetodryas carinatus*; Lönnberg, 1896:37

Chironius exoletus; Hoge, Romano & Cordeiro, 1976/77:41

Chironius carinatus; Cunha & Nascimento [partim] 1978:60

Diagnose — Nasal dividido, às vezes imperceptível; loreal mais longo que alto; órbita com diâmetro maior que sua distância da narina (borda posterior, às vezes borda anterior); 1 pré e 2 postoculares, às vezes 3 postoculares, raramente 2 pré e 2 postoculares; temporais, 1+2, rara-

TABELA 2
Chironius fuscus — Pará

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infer. Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anal	Cordeiro
446	Entrada do Piriró São Castano	02/70	♀	10-10-10	143	1	—	9 9	10 10	22 0	595	—	1 + 2	1 + 1	1 + 1		Nascimento
1 032	Fazenda Real	12 71	♀	10-10-10	145	1	—	9 9	10 10	21 4	640	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 201	Araial do Carmo	03/72	♂	10-10-10	152	1	125 125	9 9	10 10	25 0	789	419	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 300	Beia Vista	04/72	♂	10-10-10	149	1	115/115	9 9	10 10	29 0	820	440	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 311	Beia Vista	04/72	♀	10-10-10	146	1	—	9 9	10 10	19 3	530	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 475	Boa Vista	05/72	♀	10-10-10	145	1	129/129	9 9	10 10	19 0	436	263	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 486	Boa Vista	05/72	♀	10-10-10	144	1	127/127	9 9	10 10	23 0	620	370	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 729	Beia Vista	06/72	♂	10-10-10	153	1	117/117	9 9	10 10	27 4	430	275	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 751	Fazenda Real	06/72	♂	10-10-10	153	1	—	9 9	11/11	25 3	726	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
1 754	Fazenda Real	06/72	♂	10-10-10	147	1	125 125	9 9	10 10	27 4	812	460	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 053	Iha do Mosqueteiro	09/72	♂	10-10-10	148	1	124 124	9 9	10 10	15 0	730	174	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 130	Santa Luzia	09/72	♂	10-10-10	150	1	126/126	9 9	10 10	15 0	270	150	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 238	Beia Vista	09/72	♂	10-10-10	151	1	125 125	9 9	10 10	26 5	850	470	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 382	Santo Antônio do Tauá	01/73	♀	10-10-10	144	1	127/121	9 9	10 10	21 7	598	350	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 506	Beia Vista	01/73	♂	10-10-10	151	1	125 125	9 9	10 10	32 0	955	493	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 507	Beia Vista	01/73	♂	10-10-10	150	1	120/121	9 9	10 11	29 0	842	436	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 508	Beia Vista	01/73	♀	10-10-10	151	1	—	9 9	10 11	23 4	665	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 697	Boa Vista	03/73	♀	10-10-10	147	1	125/125	9 9	10 10	24 4	665	400	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
2 887	Santa Luzia	03/73	♂	10-10-9	154	1	—	9 9	10 10	24 6	720	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 067	Beia Vista	03/73	♂	10-10-10	151	1	120 120	9 9	10 10	15 0	234	114	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 124	Fazenda Real	03/73	♀	10-10-10	148	1	—	9 9	10 10	23 0	602	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 231	Peixe-Boi	03/73	♂	10-10-10	152	1	121/121	9 9	10 10	28 0	710	305	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 233	Peixe-Boi	03/73	♂	10-10-10	150	1	127/127	9 9	10 10	24 6	685	387	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 210	Peixe-Boi	03/73	♂	10-10-10	144	1	127/127	9 9	9 9	17 6	430	260	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 658	Beia Vista	05/73	♀	10-10-10	148	1	123 123	9 9	10 10	28 0	765	400	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 727	Fazenda Real	05/73	♀	10-10-10	145	1	—	9 9	10 10	15 0	348	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
3 749	Fazenda Real	05/73	♀	10-10-10	145	1	—	9 9	10 10	25 0	630	—	1 + 2	1 + 1	1 + 1		Cunha & Nascimento
4 164	Trombetinha	07/73	♂	10-10-10	150	1	126/126	9 9	10 10	22 0	640	362	1 + 2	1 + 1	1 + 1		Cunha & Nascimento

Chironius fuscus — Pará

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anel	Coloriz
5.138	Colônia Nova	10/73	♂	10-10-10	149	1	119/118	9/9	10/10	23.6	704	374		1+2	1+1		Cunha
5.173	Colônia Nova	10/73	♀	10-10-10	147	1	—	9/9	10/10	15.0	305	—		1+2	1+1		Cunha
5.175	Colônia Nova	10/73	♂	10-10-10	150	1	117/117	9/10	10/10	18.0	380	197		1+2	1+1		Cunha
5.218	Bela Vista	10/73	♂	10-10-10	145	1	—	9/9	10/10	27.5	812	—		1+3 1+2	1+1		Cunha & Nascimento
5.228	Bela Vista	10/73	♀	10-10-10	147	1	124/124	9/9	10/10	26.0	725	425		1+2	1+1		Cunha & Nascimento
5.488	Ilha do Mosqueteiro	01/74	♂	10-10-9	152	1	—	9/9	10/10	14.5	713	—		1+2	1+1		Cunha & Nascimento
5.471	Ilha do Mosqueteiro	01/74	♂	10-10-10	149	1	—	9/9	8/9	18.0	508	—		1+2	1+1		Nascimento
5.628	Santa Rosa Estr. da Vigia	03/74	♂	10-10-10	140	1	123/123	9/9	10/10	24.0	710	375		1+2	1+1		Cunha & Barata
5.645	Santa Rosa Estr. da Vigia	03/74	♀	10-10-10	144	1	123/123	9/9	10/10	24.3	710	385		1+2	1+1		Cunha & Barata
5.710	Santo Antônio do Tauá	03/74	♂	10-10-9	150	1	123/123	8/9	10/10	22.7	630	343		1+2	1+1		Cunha & Barata
6.040	Santa Luiza	03/74	♂	10-10-9	153	1	123/123	9/9	10/10	24.0	715	380		1+2	1+1		Cunha & Nascimento
6.797	Santa Rosa	07/74	♀	10-10-10	144	1	117/117	9/9	10/10	12.7	222	120		1+2	1+1		Cunha & Nascimento
6.835	Capitão Poço	03/74	♂	10-10-10	152	1	120/120	9/9	10/10	27.7	887	457		1+2	1+1		Cunha & Nascimento
7.301	Bela Vista	07/74	♂	10-10-9	150	1	—	9/9	10/10	13.7	252	—		1+2	1+1		Cunha & Nascimento
7.345	Bela Vista	07/74	♂	10-10-10	148	1	126/126	9/9	10/10	17.6	420	235		1+2	1+1		Cunha & Nascimento
7.368	Bela Vista	07/74	♀	10-10-10	150	1	130/130	9/9	11/11	24.5	645	393		1+2	1+1		Cunha & Nascimento
7.370	Bela Vista	07/74	♀	10-10-10	151	1	127/127	9/9	10/10	22.0	570	335		1+2	1+1		Cunha & Nascimento
7.374	Bela Vista	07/74	♀	10-10-10	148	1	127/127	9/9	10/10	22.0	628	375		1+2	1+1		Cunha & Nascimento
7.730	Colônia Nova	07/74	♀	10-10-10	152	1	—	9/9	10/10	24.4	630	—		1+2	1+1		Cunha & Nascimento
9.261	Santa Rosa	08/75	♀	10-10-10	143	1	127/127	9/9	10/10	18.6	487	79		1+2	1+1		Cunha & Rosemiro
9.418	Igarapé Pirajaurá	06/75	♀	10-10-10	146	1	121/121	9/8	10/10	19.5	608	346		1+2	1+1		Cunha & Rosemiro
9.423	Tomé-Açu	06/75	♀	10-10-10	149	1	126/126	9/9	10/10	21.0	600	330		1+2	1+1		Cunha & Rosemiro
8.755	Km 74 da BR-316	06/75	♂	10-10-10	147	1	120/120	8/9	11/11	27.3	765	497		1+2	1+1		Cunha & Rosemiro
9.757	Km 74 da BR-316	06/75	♂	10-10-9	150	1	120/120	9/9	10/10	29.0	760	405		1+2	1+1		Cunha & Rosemiro
10.085	Curupati	02/75	♀	10-10-10	144	1	127/127	8/9	10/10	20.7	589	370		1+2	1+1		Cunha & Rosemiro
10.710	Colônia Nova	06/75	♀	10-10-10	152	1	—	9/8	10/10	19.0	545	—		1+2	1+1		Cunha & Rosemiro
10.975	Km 11 da PA-332	02/76	♂	10-10-10	146	1	—	9/9	10/10	27.3	857	—		1+2	1+1		Cunha & Nascimento
11.276	Bela Vista	02/76	♀	10-10-10	145	1	122/122	9/9	10/10	22.0	582	335		1+2	1+1		Cunha & Nascimento

Chironius fuscus — Pará

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrais	Anal	Subaud.	Sup. Labial	Intra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Destiço	Ocular	Anel	Temp.	Coletor
11.280	Bela Vista	02/76	♀	10-10-10	148	1	120/129	9/9	11/10	26.0	739	405		1+2	1+1		Cunha & Nascimento
11.283	Bela Vista	02/76	♀	10-10-10	150	1	—	9/9	10/11	26.0	705	—		1+2	1+1		Cunha & Nascimento
11.372	Bom Jesus	11/75	♂	10-10-10	147	1	123/123	9/9	10/10	14.0	250	130		1+2	1+1		Cunha & Nascimento
11.382	Bom Jesus	11/75	♂	10-10-10	151	1	—	9/9	10/10	22.0	849	—		1+2	1+1		Cunha & Nascimento
11.801	Macapuzinho	05/76	♂	10-10-10	147	1	124/124	9/9	10/10	27.0	900	478		1+2	1+1		Cunha & Nascimento
11.869	Pratinha	03/76	♀	10-10-10	147	1	—	9/9	10/10	21.5	857	—		1+2	1+1		Cunha & Nascimento
11.887	Santa Rosa — Vigia	05/76	♀	10-10-10	147	1	129/129	9/9	10/10	30.0	565	355		1+2	1+1		Cunha & Nascimento
12.568	Bela Vista	06/76	♀	10-10-10	150	1	—	9/9	10/10	28.0	710	—		1+2	1+1		Cunha & Nascimento
12.569	Bela Vista	06/76	♀	10-10-10	145	1	126/126	9/9	10/10	21.0	630	390		1+2	1+1		Cunha & Nascimento
12.570	Bela Vista	06/76	♂	10-10-10	154	1	—	9/9	10/10	27.0	785	—		1+2	1+1		Cunha & Nascimento
12.578	Santa Rosa — Vigia	09/76	♂	10-10-10	143	1	—	9/9	9/10	25.5	715	—		1+2	1+1		Cunha & Nascimento
13.147	Bela Vista	10/76	♀	10-10-10	148	1	—	9/9	10/10	26.0	652	—		1+2	1+1		Cunha & Nascimento
13.190	Bela Vista	10/76	♂	10-10-10	152	1	127/127	9/9	11/11	26.4	743	412		1+2	1+1		Cunha & Nascimento
14.443	Santa Luzia	02/78	♀	10-10-9	145	1	—	9/9	10/10	23.6	616	—		1+2	1+1		Cunha & Nascimento

Chironius fuscus — Amapá

180	Serra do Navio	07/64	♀	10-10-10	142	1	126/126	9/9	10/11	23.0	570	360		1+2	1+1		Lério Gomes
431	Irapuá Água Branca	10/69	♂	10-10-9	147	1	—	9/9	9/9	32.5	985	—		1+2	1+1		Nascimento

Chironius fuscus — Maranhão

11.156	Nova Vida	02/76	♂	10-10-10	154	1	122/122	9/9	10/10	32.0	1.023	494		1+2	1+1		Cunha & Nascimento
12.124	Nova Vida	06/76	♀	10-10-10	147	1	130/130	9/9	10/10	23.0	691	387		1+2	1+1		Cunha & Nascimento
12.125	Nova Vida	06/76	♀	10-10-10	151	1	126/126	9/9	10/10	22.5	602	346		1+2	1+1		Cunha & Nascimento
12.731	Nova Vida	10/76	♀	10-10-10	147	1	124/124	9/9	10/10	25.4	722	495		1+2	1+1		Cunha & Nascimento
15.769	Nova Vida	09/79	♂	10-10-10	146	1	123/123	9/9	10/10	21.0	572	324		1+2	1+1		Nascimento & Esplanado

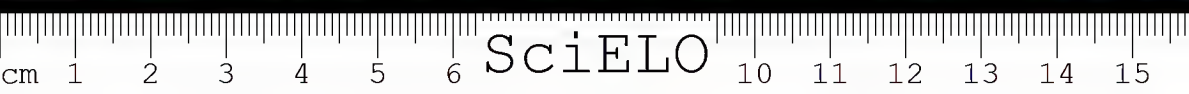
mente 1+1 ou 2+2; supralabiais 9-9, às vezes 8-9, 9-10, 8-8, 10-10 (4.º, 5.º e 6.º normalmente, 5.º e 6.º, 6.º e 7.º ou 5.º, 6.º e 7.º às vezes, tocando a órbita); infralabiais 10-10 normalmente, às vezes 11-11, 9-9, 9-10, 10-11, 10-12, 11-12 (normalmente 5 em contato com o mental anterior, às vezes 5-6 ou 6, ou ainda 4-5); mentais anteriores um pouco mais curtos que os posteriores. Escamas dorsais grandes normalmente em 12-12-10 séries longitudinais, (às vezes em 12-12-8, 14-12-10, 13-12-10 e 14-12-9), com duas linhas de carenas vertebrais (o restante lisas) muito débeis nas fêmeas, às vezes só em algumas porções do dorso; as escamas laterais acentuadamente oblíquas; fossetas apicilares presentes na região nugal e pescoço, às vezes até quase a metade do corpo, apenas em algumas escamas, espaçando e retornando a aparecer no resto do corpo e quase toda a cauda, em geral com uma fosseta em cada escama (às vezes duas). Anal dividida. Dentes maxilares 26-30. Ventrais 139-160, machos 141-154, fêmeas 139-160; caudais divididas, machos 121-148, fêmeas 120-143. Comprimento máximo do indivíduo n.º 14.643 ♀ de Gancho do Arará, Maranhão, corpo 810 mm, cauda 480 mm, total 1.290 mm.

Colorido em vida: Parte superior da cabeça pardacento, tingido de vermelho e amarelado nos parietais e região nugal; uma tênue faixa clara vertebral, com uma orla enegrecida de cada lado, nos lados amarelo abrangendo os supralabiais; focinho avermelhado, (rostral e nasais); parte inferior amarelo vivo, abrangendo os gulares, mentais e até cerca de 30 ventrais, estando o resto do ventre com um amarelo claro, até a região anal; cauda amarelo vivo idêntico à parte inferior da cabeça. Dorso pardo oliváceo, tendendo ao amarelado indiviso, próximo às ventrais, na extensão do corpo e cauda. Pescoço de tom azeitonado mais distinto que o resto do corpo. Olho com um círculo amarelo em torno da pupila.

Colorido em preservativo: No aspecto geral o tom que se observa é o cinéreo no dorso e lados do corpo e cauda, com as escamas apresentando uma bordadura azul escurecido, dando uma aparência reticulada; uma tênue faixa clara vertebral orlada de pardo escuro. Parte anterior da cabeça cinérea e a posterior e nuca esbranquiçados, assim como os lados, labiais, e toda parte inferior do corpo e cauda.

Comentários — Esta espécie Lineana recentemente exumada por Hoge, Romano & Cordeiro (1976/77:41) vinha sendo confundida com *Chinorius carinatus* (Linnaeus) há cerca de um século e meio, desde os tempos de Wagler (1830). A denominação dada por Linnaeus para a presente espécie foi válida como demonstram os autores citados, e nós com a análise efetuada em 154 exemplares de várias procedências do Pará, Amapá, Maranhão e Mato Grosso (Aripuanã). Os caracteres são perfeitamente distintos dos encontrados nas outras espécies de *Chironius*.

Apesar disso, Cunha e Nascimento (1978:60) também incorreram no erro, que guiando-se pelos autores anteriores consideraram a maioria dos exemplares estudados como sendo *C. carinatus*, em flagrante desacordo, pois esta é quase rara no leste do Pará enquanto *C. exoletus* é a espécie dominante e muito freqüente neste Estado e Maranhão, em relação a todas as outras representantes do gênero. Tendo em vista o volumoso



material analisado neste trabalho (apenas uma seleção da coleção existente na Seção de Herpetologia) e o pequeno material estudado por Hoge, Romano & Cordeiro (1976/77:41) podemos admitir que *C. exoletus* está distribuída por toda a Amazônia hileiana e talvez Guianas.

Em Gasc & Rodrigues (1980:571) encontra-se espécie *C. carinatus* para a Guiana Francesa, contudo há possibilidade de aí ocorrer *C. exoletus*, se admitirmos os dados merísticos apontados. No mesmo caso encontram-se as observações de Dixon & Soini (1977:39) ao identificarem *C. carinatus* para a região de Iquitos, Peru. Os dados merísticos mostrados pelos autores, fazem supor que no grupo de 28 exemplares analisados, todos ou muitos deles seriam de fato *C. exoletus*, considerando-se em particular as dorsais, ventrais, caudais, supralabiais e mais acentuadamente os dentes maxilares (26-31) idênticos na variação dos exemplares estudados por Hoge, Romano & Cordeiro (1976/77:41) e nós.

Dos 154 exemplares analisados neste trabalho, 67 são machos e 87 fêmeas. O dimorfismo sexual é pouco acentuado, sendo contudo mais perceptível em alguns caracteres como as duas nítidas carenas vertebrais nos machos, enquanto muito débeis nas fêmeas; escamas ventrais um pouco menores nos machos com as caudais pouco acima das fêmeas.

Para definir melhor a área de ocorrência de *C. exoletus* incluímos na análise os exemplares disponíveis na Seção de Herpetologia, coletados em diversos locais da Amazônia, além dos do Pará, Amapá e Maranhão, como Aldeia dos índios Guajajara, cerrados do Maranhão e Cachoeira Dardanelos no rio Aripuanã, Mato Grosso.

A espécie vive em todos os ambientes como floresta primária, capoeiras e roçados, igapó, campos e cerrados. Possui hábitos semi-arborícolas e terrestres. Alimenta-se especialmente de Anfíbios (rãs, *Hyla*, *Leptodactylus?*, salamandra *Bolitoglossa altamazonica* (Cope, 1874) e sapos e lagartos (*Thecadactylus rapicaudus* (Houttuyn, 1782), conforme análise do conteúdo estomacal. Quantitativamente a preferência é para certas espécies de rãs, do gênero *Hyla*, também observados por Dixon & Soini (1977:39) para espécies do Peru identificados como *C. carinatus* (= *C. exoletus* ?).

Material examinado — Verificar tabela anexa.

Chironius exoletus

Chironius carinatus (Linnaeus)

Coluber carinatus Linnaeus, 1758, 10:223. Localidade típica: Indiis (in error)

Herpetodryas carinatus; Boulenger, 1894 [partim] :73; Gomes, 1918b, [partim] :66.

Chironius carinatus; Ruthven, 1922:65; Amaral, 1930, 4:160; Hoge, 1964:53; Cordeiro & Hoge, 1973:265; Cunha & Nascimento, 1978 [partim] :60, Est. VIII, fig. 1.

Diagnose — Nasal dividido; loreal mais longo que larga; órbita com diâmetro maior que sua distância da narina; 1 pré e 2 postoculares,

TABELA 3
Chironius exoletus — Amapá

Nº	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infr. Labial	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Anal	Temp.	Coletor
73	Rio Tracajuba	09/76	♀	12-12-10	146	1/1	—	9/9	11/11	26.3	628	—	1+2	1+2	1+2		P. Vasconcelos
Chironius exoletus — Mato Grosso																	
10-418	Cabeceira Dardendo Rio Ariguanã	10/77	♀	12-12-10	154	1/1	143/143	9/9	10/11	34.0	726	445	1+2	1+2	1+2		Moriera
Chironius exoletus — Pará																	
7-461	Km 11 da Estrada do Acará	07/74	♀	14-12-10	150	1/1	—	8/9	9/10	31.8	707	—	1+2	1+2	1+2		Cunha & Nascimento
8-673	Km 16 da Estrada do Acará	02/76	♂	12-12-10	142	1/1	137/137	9/9	10/10	21.0	436	276	1+2	1+2	1+2		Cunha & Nascimento
8-686	Km 16 da Estrada do Acará	02/75	♀	12-12-10	151	1/1	—	9/9	10/10	23.0	697	—	1+2	1+2	1+2		Cunha & Nascimento
8-706	Km 16 da Estrada do Acará	02/75	♀	12-12-9	144	1/1	130/130	9/10	10/10	29.0	713	400	1+2	1+2	1+2		Cunha & Nascimento
9-473	Km 01 da PA-332	06/75	♀	12-12-10	151	1/1	137/137	9/9	10/10	29.6	628	375	1+2	1+2	1+2		Cunha & Nascimento
9-491	Km 11 da PA-332	06/75	♀	14-12-10	152	1/1	136/136	9/10	10/12	29.5	710	393	1+2	1+2	1+2		Cunha & Nascimento
10-817	Rio Fira-Juara	10/75	♀	14-12-10	153	1/1	—	9/9	10/10	30.5	676	—	2+2	1+2	1+2		Cunha & Nascimento
10-927	Rio Fira-Juara	02/76	♂	12-12-8	145	1/1	—	8/8	10/10	27.8	603	—	1+2	1+2	1+2		Cunha & Nascimento
10-954	Km 16 da Estrada do Acará	02/76	♀	12-12-10	146	1/1	127/127	9/9	10/10	30.0	757	397	1+2	1+1	1+2		Cunha & Nascimento
10-959	Km 16 da Estrada do Acará	02/76	♂	14-12-10	148	1/1	136/136	9/9	11/11	22.8	665	405	1+2	1+2	1+2		Cunha & Nascimento
10-976	Km 16 da Estrada do Acará	02/76	♀	14-12-8	152	1/1	143/143	9/9	10/10	28.8	664	416	1+2	1+2	1+2		Cunha & Nascimento
11-704	Km 16 da Estrada do Acará	06/76	♂	12-12-10	142	1/1	135/135	9/9	10/10	28.8	660	410	1+2	1+2	1+2		Cunha & Nascimento
11-730	Km 12 da PA-15 Concórdia — Tomá-Açu	06/76	♂	12-12-10	142	1/1	131/131	8/8	10/10	31.2	691	390	1+2	1+2	1+2		Cunha & Nascimento
11-786	Porto Jarbas Passarinho	06/76	♂	12-12-8	148	1/1	140/140	9/9	10/10	26.5	694	409	1+2	1+2	1+2		Cunha & Nascimento
11-787	Porto Jarbas Passarinho	06/76	♀	12-12-10	154	1/1	132/132	9/9	10/9	27.0	685	343	1+2	1+2	1+2		Cunha & Nascimento
11-788	Porto Jarbas Passarinho	06/76	♀	12-12-10	152	1/1	—	9/9	11/11	26.4	619	—	1+2	1+2	1+2		Cunha & Nascimento
11-789	Porto Jarbas Passarinho	06/76	♀	14-12-10	157	1/1	136/136	9/9	10/10	26.4	690	387	1+2	1+2	1+2		Cunha & Nascimento
11-790	Porto Jarbas Passarinho	06/76	♂	12-12-10	154	1/1	137/137	9/9	10/10	29.0	724	422	1+2	1+2	1+2		Cunha & Nascimento
12-747	Porto Jarbas Passarinho	09/76	♀	12-12-10	153	1/1	133/133	9/9	11/11	27.0	660	395	1+2	1+2	1+2		Cunha & Nascimento
12-748	Porto Jarbas Passarinho	09/76	♂	12-12-10	145	1/1	134/134	9/9	11/11	31.0	716	340	1+2	1+2	1+2		Cunha & Nascimento
12-749	Porto Jarbas Passarinho	09/76	♂	12-12-10	150	1/1	—	9/9	11/11	26.2	675	—	1+2	1+2	1+2		Cunha & Nascimento
12-787	Km 16 da Estrada do Acará	09/76	♂	12-12-10	146	1/1	—	8/8	9/10	32.2	697	—	1+2	1+2	1+2		Cunha & Nascimento
12-788	Km 16 da Estrada do Acará	09/76	♀	12-12-10	150	1/1	132/132	8/9	10/10	32.4	655	362	1+2	1+2	1+2		Cunha & Nascimento
12-940	Porto Jarbas Passarinho	06/76	♂	12-12-10	153	1/1	135/135	9/9	10/10	31.5	778	461	1+2	1+2	1+2		Cunha & Nascimento
12-941	Porto Jarbas Passarinho	06/76	♂	12-12-10	148	1/1	138/138	9/10	10/10	31.5	769	438	1+2	1+2	1+2		Cunha & Nascimento

CUNHA, O. R. & NASCIMENTO, F. P. Ofídios da Amazônia. XV. As espécies de *Chironius* da Amazônia Oriental (Pará, Amapá e Maranhão). (Ophidia: Colubridae). *Mem. Inst. Butantan*, 46:139-172, 1982.

TABELA 3 (cont.)
Chironius exotici — Pará

Nº	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Penitção	Ocular	Temp.	Aoel	Color
12.942	Porto Jarbas Passarinho	06/76	♀	12-12-10	137	1-1	—	9/9	10/10	27,8	540	—	—	1+2	1+2	—	Cunha & Nascimento
12.943	Porto Jarbas Passarinho	06/76	♂	12-12-10	147	1-1	138/128	9/9	10/10	28,0	623	369	—	1+2	1+2	—	Cunha & Nascimento
12.944	Porto Jarbas Passarinho	06/76	♀	12-12-10	151	1-1	—	9/9	10/10	29,0	636	—	—	1+2	1+2	—	Cunha & Nascimento
12.959	Porto Jarbas Passarinho	06/76	♀	12-12-10	153	1-1	137/137	9/9	10/10	25,0	629	368	—	1+2	1+2	—	Cunha & Nascimento
12.960	Porto Jarbas Passarinho	06/76	♀	12-12-10	150	1-1	118/118	9/9	10/11	28,0	690	373	—	1+2	1+2	—	Cunha & Nascimento
13.269	Povoação do Lito	10/77	♀	12-12-10	152	1-1	127/127	9/9	10/10	30,3	677	377	—	1+2	1+2	—	Cunha & Nascimento
13.357	Itapuzza	10/77	♀	12-12-10	144	1-1	—	9/9	10/10	21,3	449	—	—	1+2	1+2	—	Cunha & Nascimento
13.362	Sítio Bela Vista	10/77	♀	12-12-10	153	1-1	136/136	9/9	9/9	28,0	645	370	—	1+2	1+2	—	Cunha & Nascimento
13.401	PA-332 Sítio Bela Vista	10/77	♀	12-12-10	156	1-1	125/126	9/9	10/10	33,0	735	393	—	1+3	1+2	—	Cunha & Nascimento
13.416	PA-332 Sítio Bela Vista	10/77	♀	12-12-10	147	1-1	130/130	9/9	10/10	30,0	700	385	—	1+2	1+2	—	Cunha & Nascimento
14.262	Km 16 da Estrada do Acará	02/78	♀	12-12-10	145	1-1	—	9/9	11/11	29,7	721	—	—	1+2	1+2	—	Cunha & Nascimento
14.483	Km 10 da Estrada do Acará	07/78	♂	12-12-10	143	1-1	—	9/9	10/10	29,3	564	—	—	1+2	1+2	—	Cunha & Nascimento
14.484	Km 14 da Estrada do Acará	07/78	♀	12-12-10	147	1-1	120/121	9/9	10/10	25,4	522	299	—	1+2	1+2	—	Cunha & Nascimento
14.514	PA-332 Sítio Bela Vista	07/78	♀	12-12-10	149	1-1	—	9/9	10/10	31,3	718	—	—	1+2	1+2	—	Cunha & Nascimento
14.515	PA-332 Sítio Bela Vista	07/78	♀	12-12-10	153	1-1	—	9/9	10/10	32,7	762	—	—	1+2	1+2	—	Cunha & Nascimento
14.521	Km 11 da PA-332	07/78	♀	12-12-10	152	1-1	—	9/9	10/10	33,6	810	—	—	1+2	1+2	—	Cunha & Nascimento
14.954	Km 16 da Estrada do Acará	08/78	♂	12-12-8	141	1-1	135/135	8/8	9/9	29,4	674	409	—	1+2	1+2	—	Cunha & Nascimento
15.166	Km 11 da PA-332	10/77	♀	12-12-10	143	1-1	131/131	9/9	10/10	31,4	280	412	—	1+2	1+2	—	Cunha & Nascimento
15.311	Porto Jarbas Passarinho	02/78	♀	12-12-10	152	1-1	132/132	9/9	11/11	28,0	689	375	—	1+2	1+2	—	Cunha & Nascimento
15.312	Porto Jarbas Passarinho	02/78	♀	12-12-10	149	1-1	—	9/9	10/10	30,5	699	—	—	1+2	1+2	—	Cunha & Nascimento
15.501	Km 16 da Estrada do Acará	08/79	♀	12-12-10	147	1-1	—	9/9	10/10	25,6	697	—	—	1+2	1+2	—	Cunha & Nascimento
15.505	Km 16 da Estrada do Acará	08/79	♂	12-12-10	144	1-1	142/142	9/9	10/10	24,2	612	383	—	1+3	1+2	—	Cunha & Nascimento
15.548	Porto Jarbas Passarinho	08/79	♂	12-12-10	154	1-1	140/140	10/10	10/10	22,4	668	354	—	1+2	1+2	—	Cunha & Nascimento
15.549	Porto Jarbas Passarinho	08/79	♂	12-12-8	151	1-1	—	9/9	10/10	28,5	766	—	—	1+2	1+2	—	Cunha & Nascimento
16.102	PA-332 Sítio Bela Vista	01/80	♀	14-12-10	152	1-1	—	9/9	10/10	28,0	616	—	—	1+2	1+2	—	Cunha & Nascimento
16.105	PA-332 Sítio Bela Vista	01/80	♀	12-12-8	150	1-1	—	9/9	11/12	14,0	252	—	—	1+2	1+2	—	Cunha & Nascimento
31	—	01/81	♀	12-12-10	145	1-1	—	9/9	11/11	28,4	788	—	—	1+2	1+2	—	—
400	Estrada do Faltão Santarem	08/69	♂	14-12-10	150	1-1	142/142	9/9	10/11	13,0	258	150	—	1+2	1+2	—	Milton
15.550	Portel	03/80	♀	12-12-10	153	1-1	—	9/9	11/11	31,8	764	—	—	1+2	1+2	—	Princípio Fôres
16.381	Cachoeira do Arari (Iha do Marajó)	08/81	♀	14-12-10	153	1-1	134/134	9/10	11/10	30,6	765	430	—	1+2	1+2	—	Princípio Fôres
465	Boa Vista — Apeú	05/70	♀	14-12-10	150	1-1	—	10/9	10/10	29,0	649	—	—	1+2	1+2	—	Cunha & Nascimento
468	Boa Vista — Apeú	05/70	♀	12-12-10	142	1-1	141/141	9/9	11/11	31,0	750	445	—	1+2	1+2	—	Cunha & Nascimento
539	Boa Vista — Apeú	02/71	♀	12-12-8	144	1-1	134/135	9/9	10/10	29,6	737	423	—	1+2	1+2	—	Cunha & Nascimento
557	Iha de Mosquito	03/71	♀	12-12-10	142	1-1	138/138	9/9	10/10	25,6	613	397	—	1+2	1+2	—	Milton

TABELA 3 (cont.)
Chironius exoletus — Pará

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrais	Anal	Subcaud.	Sup. Labial	Ínfra- Lab.	C. Cabeça (mm)	C. Corpo (mm)	C. Cauda (mm)	Dentição	Ocular	Temp.	Avul	Color
786	Fazenda Real	09/71	♀	12-12-10	149	1/1	120/130	9/9	10/10	31.0	738	337		1+2	1+2		Cunha & Nascimento
1.068	Fazenda Real	11/71	♂	12-12-8	151	1/1	135/135	9/9	10/10	28.4	710	415		1+2	1+2		Cunha & Nascimento
1.158	Boa Vista — Apeú	03/72	♀	14-12-10	150	1/1	135/135	9/9	11/11	37.5	600	390		1+2	1+2		Cunha & Nascimento
1.216	Illa de Mosquito	03/72	♀	12-12-9	150	1/1	123/123	9/9	11/11	30.0	722	382		1+2	1+2		Cunha & Nascimento
1.343	Fazenda Real	04/72	♂	12-12-8	144	1/1	—	9/9	10/10	28.4	735	—		1+2	1+2		Cunha & Nascimento
1.344	Fazenda Real	04/72	♂	12-12-10	149	1/1	—	9/9	10/9	23.4	600	—		1+2	1+2		Cunha & Nascimento
1.427	Illa de Mosquito	05/72	♀	12-12-10	153	1/1	—	8/8	10/9	24.0	518	—		1+2	1+2		Cunha & Nascimento
1.550	Boa Vista — Apeú	06/72	♀	12-12-10	152	1/1	138/138	9/9	11/11	29.0	677	400		1+2	1+2		Cunha & Nascimento
1.749	Fazenda Real	06/72	♂	12-12-8	148	1/1	—	9/9	9/10	29.0	731	—		1+2	1+2		Cunha & Nascimento
2.017	Boa Vista — Apeú	06/72	♂	12-12-10	142	1/1	136/136	9/9	10/12	30.5	743	453		1+2	1+2		Cunha & Nascimento
3.094	Fazenda Real	03/73	♀	12-12-10	146	1/1	133/133	9/9	10/11	31.5	683	195		1+2	1+2		Cunha & Nascimento
3.121	Fazenda Real	03/73	♀	12-12-10	150	1/1	132/132	9/9	10/10	31.0	650	397		1+2	1+2		Cunha & Nascimento
3.123	Fazenda Real	03/73	♂	12-12-8	144	1/1	—	9/9	11/10	27.7	715	—		1+2	1+2		Cunha & Nascimento
3.129	Fazenda Real	03/73	♀	12-12-10	165	1/1	—	9/9	11/11	24.0	575	—		1+2	1+2		Cunha & Nascimento
3.255	Fazenda Real	09/73	♀	12-12-10	145	1/1	—	9/9	11/11	25.0	619	—		1+2	1+2		Cunha & Nascimento
3.256	Fazenda Real	09/73	♀	12-12-10	150	1/1	131/131	9/9	10/11	22.6	600	346		1+2	1+2		Cunha & Nascimento
3.750	Fazenda Real	06/73	♂	12-12-10	145	1/1	132/132	9/9	10/10	28.0	709	417		1+2	1+2		Cunha & Nascimento
3.751	Fazenda Real	05/73	♂	12-12-10	143	1/1	136/136	9/9	11/11	26.0	600	375		1+2	1+2		Cunha & Nascimento
4.044	Boa Vista — Apeú	07/73	♂	12-12-10	144	1/1	—	9/9	11/11	31.4	784	—		1+2	1+2		Cunha & Nascimento
4.501	Fazenda Real	07/73	♂	12-12-10	149	1/1	139/139	9/9	11/11	38.0	712	435		1+2	1+2		Cunha & Nascimento
4.512	Fazenda Real	07/73	♂	12-12-8	146	1/1	136/136	9/9	10/10	29.0	720	430		1+2	1+2		Cunha & Nascimento
5.281	Fazenda Real	10/73	♀	12-12-10	150	1/1	131/131	9/9	10/10	30.0	708	403		1+2	1+2		Cunha
5.286	Fazenda Real	10/73	♀	12-12-10	150	1/1	—	9/9	10/10	28.7	714	—		1+2	1+2		Cunha
5.467	Illa de Mosquito	01/74	♀	14-12-10	159	1/1	—	9/9	11/11	30.0	675	—		1+2	1+2		Cunha & Nascimento
5.470	Illa de Mosquito	01/74	♀	12-12-8	144	1/1	—	9/9	10/11	28.7	690	—		1+2	1+2		Cunha & Nascimento
5.720	Boa Vista — Apeú	03/74	♀	12-12-10	146	1/1	137/137	9/9	11/10	25.5	555	340		1+2	1+2		Cunha & Nascimento
5.7.5	Boa Vista — Apeú	03/74	♀	12-12-8	143	1/1	139/139	9/9	10/10	27.7	698	415		1+2	1+2		Cunha & Nascimento
6.921	Boa Vista — Apeú	07/74	♂	12-12-10	141	1/1	127/127	9/9	10/10	26.0	600	350		1+2	1+2		Cunha & Nascimento
6.933	Boa Vista — Apeú	07/74	♂	12-12-8	144	1/1	132/132	9/9	11/11	31.5	762	441		1+2	1+2		Cunha & Nascimento
9.444	Boa Vista — Apeú	06/75	♀	12-12-10	153	1/1	131/131	9/9	10/10	27.5	670	390		1+2	1+2		Cunha & Nascimento
10.906	Illa de Mosquito	02/76	♀	12-12-10	145	1/1	142/142	9/9	10/11	30.0	733	441		1+2	1+2		Cunha & Nascimento
13.758	Colônia Nova	10/77	♂	12-12-8	143	1/1	—	9/9	10/11	28.2	720	—		1+2	1+2		Cunha & Nascimento
13.759	Colônia Nova	10/77	♀	14-12-10	150	1/1	—	9/9	10/10	25.7	674	—		1+2	1+2		Cunha & Nascimento

TABELA 3 (cont.)
Chironius exilis — Pará

N.º	PROCEDÊNCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infr. Labial	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anal	Color
14.019	Colônia Nova	10/77	♂	12:12-10	143	1/1	145/145	0-9	11/11	38.7	237	450	1-2	1-2	1-2		Nascimento
14.020	Colônia Nova	10/77	♀	12:12-10	145	1/1	—	0-9	11/10	30.0	736	—	1-2	1-2			Nascimento
<i>Chironius maderu</i> — Maranhão																	
10.326	Nova Vida	06/75	♀	14:12-11	148	1/1	138/138	8-8	9-8	32.6	766	403		1-2	1-2		Cunha & Reseriro
10.228	Nova Vida	06/75	♂	12:12-9	147	1/1	133/133	9/10	9-0	31.5	775	444		1-2	1-2		Cunha & Reseriro
10.259	Pará	06/75	♀	14:12-6	150	1/1	—	9-9	10-10	35.0	737	—		1-2	1-2		Cunha & Reseriro
10.857	Nova Vida	10/75	♀	14:12-10	154	1/1	138/138	9-9	10-10	26.6	700	396		1-2	1-2		Cunha & Nascimento
10.660	Nova Vida	10/75	♂	12:12-9	144	1/1	128/128	9-9	11/11	31.2	759	385		1-2	1-2		Cunha & Nascimento
11.063	Nova Vida	02/76	♂	12:12-8	147	1/1	144/144	9-9	10/10	29.4	720	447		1-2	1-2		Cunha & Nascimento
11.054	Nova Vida	02/76	♀	12:12-9	143	1/1	133/133	9-9	9-9	26.7	584	326		1-2	1-2		Cunha & Nascimento
12.022	Pará	06/76	♂	14:12-10	144	1/1	—	9-9	11/11	25.7	653	—		1-2	1-2		Cunha & Nascimento
12.023	Pará	06/76	♀	12:12-10	154	1/1	—	9-9	10/10	26.6	631	—		1-2	1-2		Cunha & Nascimento
12.243	Nova Vida	06/76	♀	12:12-8	146	1/1	136/136	9/9	10/10	29.0	746	445		1-2	1-2		Cunha & Nascimento
12.246	Nova Vida	06/76	♂	12:12-6	146	1/1	133/133	8-8	9/10	28.2	656	301		1-2	1-2		Cunha & Nascimento
12.247	Nova Vida	06/76	♂	12:12-8	155	1/1	—	9-9	10/10	31.6	580	—		1-2	1-2		Cunha & Nascimento
12.250	Nova Vida	06/78	♀	14:12-10	147	1/1	—	9-9	9/10	30.4	665	—		1-2	1-2		Cunha & Nascimento
12.252	Nova Vida	06/76	♀	12:12-10	146	1/1	—	9-9	10-9	28.7	658	—		1-2	1-2		Cunha & Nascimento
12.766	PP-316 - São Raimundo	06/76	♀	12:12-8	145	1/1	131/131	9-9	8-9	21.5	490	285		1-2	1-2		Cunha & Nascimento
12.642	Pará	06/76	♀	14:12-6	148	1/1	136/136	9-9	11/11	27.0	677	395		1-2	1-2		Cunha & Nascimento
13.615	Pará	10/77	♀	12:12-10	159	1/1	—	9-9	10-11	23.6	594	—		1-2	1-2		Nascimento
13.616	Pará	10/77	♀	12:12-10	151	1/1	141/141	9-9	10-11	22.4	500	294		1-2	1-2		Nascimento
13.617	Pará	10/77	♀	14:12-10	148	1/1	143/143	9-9	10/10	31.4	769	455		1-2	1-2		Nascimento
13.616	Pará	10/77	♀	12:12-10	145	1/1	146/146	9-9	10-10	24.4	567	362		1-2	1-2		Nascimento
13.619	Pará	10/77	♀	14:12-10	154	1/1	127/128	9-9	10/10	30.8	582	351		1-2	2+1		Nascimento
13.682	Nova Vida	10/77	♀	12:12-9	145	1/1	—	9-9	10-10	25.7	555	—		1-2	1-2		Nascimento
13.683	Nova Vida	10/77	♀	12:12-10	143	1/1	—	9-9	11/11	26.0	531	—		1-3	1-2		Nascimento
13.686	Nova Vida	10/77	♀	12:12-10	149	1/1	—	9-9	9-9	28.6	660	—		1-2	1-2		Nascimento
14.252	Pará	02/78	♀	14:12-10	152	1/1	—	9-9	10/10	32.3	799	—		1-2	1-2		Cunha & Nascimento
14.253	Pará	02/78	♂	14:12-10	154	1/1	138/138	9/10	11/11	29.7	665	366		1-2	1-2		Cunha & Nascimento
14.254	Pará	02/78	♀	12:12-10	156	1/1	134/134	9-9	0-10	28.6	665	392		1-2	1-2		Cunha & Nascimento
14.255	Pará	02/78	♂	14:12-9	146	1/1	137/137	9-9	10/10	22.0	482	294		1-2	1-2		Cunha & Nascimento
14.343	Pará	02/78	♂	12:12-10	143	1/1	136/136	9-9	10/10	33.0	785	455		1-2	1-2		Cunha & Nascimento
14.627	Gracho do Arari	07/78	♂	12:12-6	153	1/1	—	9-9	10/10	16.0	405	—		1-2	1-2		Cunha & Nascimento
14.660	Gracho do Arari	07/78	♂	12:12-8	161	1/1	121/121	9-9	10/10	22.0	538	292		1-2	1-2		Cunha & Nascimento
14.641	Gracho do Arari	07/78	♀	12:12-10	156	1/1	155/155	8-6	10/10	30.4	757	400		1-2	1-2		Cunha & Nascimento

TABELA 3 (cont.)
Chironius exotus — Maranhão

Nº	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anel	Coior
14.642	Gancho do Arari	07/78	♀	13-12-10	152	1/1	131-131	9/9	10/10	28.4	576	387		1+2	1+1		Cunha & Nascimento
14.643	Gancho do Arari	07/78	♀	14-12-10	152	1/1	132-132	8/9	10/11	32.8	810	480		1+2	1+2		Cunha & Nascimento
14.644	Gancho do Arari	07/78	♂	14-12-10	150	1/1	—	9/9	10/10	29.0	720	—		1+2	1+2		Cunha & Nascimento
14.671	Puraquê	07/78	♂	12-12-10	149	1/1	134-134	9/9	10/10	30.0	780	462		1+2	1+2		Cunha & Nascimento
14.672	Puraquê	07/78	♂	12-12-10	149	1/1	—	9/9	10/10	31.4	790	—		1+2	1+2		Cunha & Nascimento
14.761	Nova Vida	07/78	♀	12-12-10	147	1/1	128-128	9/9	10/10	26.5	634	370		1+2	1+2		Cunha & Nascimento
14.762	Nova Vida	07/78	♀	12-12-10	151	1/1	—	9/9	10/10	33.0	834	—		1+2	1+2		Cunha & Nascimento
14.852	Gancho do Arari	07/78	♂	12-12-8	149	1/1	—	9/9	11/11	32.0	855	—		1+2	1+2		Cunha & Nascimento
14.853	Gancho do Arari	07/78	♂	12-12-10	147	1/1	140-140	9/9	10/10	24.7	600	367		1+2	1+2		Cunha & Nascimento
14.859	Gancho do Arari	07/78	♂	13-12-10	143	1/1	—	9/9	11/11	24.7	592	—		1+2	1+2		Cunha & Nascimento
14.991	Nova Vida	10/78	♀	12-12-10	148	1/1	133-133	9/9	11/11	31.0	717	390		1+2	1+2		Nascimento & Nascimento
14.994	Nova Vida	10/78	♀	12-12-10	150	1/1	134-134	9/9	10/10	28.0	667	350		1+2	1+2		Nascimento & Nascimento
15.037	Gancho do Arari	10/78	♀	12-12-10	152	1/1	127-127	8/9	9/10	15.0	385	213		1+2	1+2		Nascimento & Nascimento
15.038	Gancho do Arari	10/78	♂	12-12-10	149	1/1	—	9/9	11/10	25.0	670	—		1+2	1+2		Nascimento & Nascimento
15.047	Pará	10/78	♂	12-12-8	146	1/1	145-148	9/9	11/11	22.5	515	328		1+2	1+2		Nascimento & Nascimento
15.562	Aldeia Sapucaia	08/79	♀	14-12-10	153	1/1	126-126	9/9	10/11	—	—	—		1+2	1+2		Nascimento & Reiginado
15.582	BR-225 - Santa Maria	08/79	♂	12-12-10	145	1/1	134-134	9/9	10/10	27.4	690	410		1+2	1+2		Nascimento & Reiginado
15.617	Gancho do Arari	08/79	♀	12-12-10	157	1/1	—	9/9	10/10	22.0	560	—		1+2	1+2		Nascimento & Reiginado
15.621	Gancho do Arari	08/79	♀	12-17-10	155	1/1	126-126	9/9	11/11	23.5	760	403		1+2	1+2		Nascimento & Reiginado
15.628	Gancho do Arari	08/79	♀	12-12-10	155	1/1	134-134	9/9	10/10	23.0	566	325		1+2	1+2		Nascimento & Reiginado
15.719	Nova Vida	08/79	♀	12-12-10	152	1/1	—	9/9	11/11	31.0	774	—		1+2	1+2		Nascimento & Reiginado
15.721	Nova Vida	08/79	♂	12-17-10	148	1/1	137-137	9/9	10/10	29.3	738	435		1+2	1+2		Nascimento & Reiginado
15.722	Nova Vida	08/79	♀	12-12-10	153	1/1	—	9/9	10/10	31.4	722	—		1+2	1+2		Nascimento & Reiginado
16.071	Gancho do Arari	08/79	♀	12-12-10	147	1/1	—	10/10	10/10	27.5	658	—		1+2	1+2		Nascimento & Reiginado
16.142	Gancho do Arari	02/80	♀	14-12-10	153	1/1	—	9/9	11/11	28.4	695	—		1+2	1+2		Cunha & Nascimento
16.174	Puraquê	02/80	♀	12-12-10	157	1/1	132-132	8/9	10/10	30.7	804	437		1+2	1+2		Cunha & Nascimento
16.175	Puraquê	02/80	♀	12-12-10	160	1/1	—	9/9	10/10	25.0	605	—		1+2	1+2		Cunha & Nascimento
16.177	Puraquê	02/80	♀	12-12-10	155	1/1	—	9/9	10/10	21.0	520	—		1+2	1+2		Cunha & Nascimento
16.208	Nova Vida	02/80	♀	14-12-10	152	1/1	—	8/8	9/10	32.3	753	—		1+2	1+1		Cunha & Nascimento

raramente 1+3; temporais 1+2, raramente 1+1 ou 1+3; supralabiais usualmente 8, às vezes 9-9 ou 8-9 (4.º e 5.º, 5.º e 6.º tocando a órbita, às vezes 4.º, 5.º e 6.º ou variando de um lado com o 4.º e 5.º ou este com o 5.º e 6.º); infralabiais 10-10 11-11, às vezes 9-10, 10-11 e 9-9 (5 em contato as mais das vezes, com as mentais anteriores, às vezes 6 ou 5-6 de um lado e do outro); mentais anteriores mais curtas que as posteriores. Escamas dorsais normalmente em 12-12-10 séries longitudinais, às 12-12-8, 12-12-9 e 14-12-10, com duas filas de escamas carenadas, fortemente nos machos, mais fracas nas fêmeas; escamas laterais acentuadamente oblíquas; fossetas apiculares presentes na região nugal e pescoço, com uma fosseta usualmente, raramente duas. Anal dividida. Dentes maxilares 30-35. Ventrais 150-161 e caudais 116 a 133 nos machos e nas fêmeas 153 a 162 ventrais e 116 a 124 caudais. Comprimento maior do exemplar completo n.º 646, macho, da Ilha do Mosqueiro (Belém) — corpo 1.304 mm e cauda 620 mm, total 1.924 mm.

O colorido em preservativo é pardo oliváceo na cabeça e região dorsal, ora mais escuro, ora mais claro; lados tendendo ao amarelado; labiais, garganta, pescoço e toda região ventral amarelo. Escamas laterais e caudais orladas de negro, de aspecto reticulado; as parvertebrais grandes não oblíquas com as margens fortemente anegradadas, estendendo-se às bordas laterais das ventrais. Caudais acentuadamente bordejadas de negro com o centro esbranquiçado, dando um aspecto bastante conspícuo.

Comentários — Esta espécie de belo aspecto e perfeitamente diferenciável das outras *Chironius*, apesar disso, tem sido confundida com *C. exoletus* e *C. scurrulus* desde Boulenger (1894:73) até Gomes (1918b:66) e Cunha & Nascimento (1978:60), entre alguns.

No trabalho sobre os ofídios do leste do Pará (Cunha & Nascimento, Id.) identificamos 226 exemplares de *Chironius carinatus*, que em verdade são agora *C. exoletus*, pois naquela ocasião não tínhamos ainda conhecimento da revalidação desta espécie por Hoge, Romano & Cordeiro (1976/77:40). A típica *C. carinatus* é rara no leste do Pará, substituída por *C. exoletus*. No trabalho acima citado a foto da Estampa 8, figura 1, é de fato um *Chironius carinatus*, coletada então na ilha de Mosqueiro (Belém).

Diferencia-se perfeitamente de *C. exoletus* por possuir denteição mais elevada, caudais mais baixas, colorido característico e alcançar geralmente maior tamanho. É também muito diferente de *C. scurrulus*, não apenas pela denteição, mais elevada nesta espécie, como pela anal inteira e colorido.

Possui distribuição geográfica ampla na América do Sul a oriente dos Andes. Ocorre em quase todo o Brasil, vivendo em floresta primária, capoeiras, cerrados, campos e caatingas. No presente trabalho foram examinados exemplares das savanas de Roraima, campos de Marajó, matas do Amapá, rio Javari (fronteira com o Peru) e capoeiras e babaquais do Maranhão. Alimenta-se exclusivamente de Anfíbios (rãs, possivelmente do gênero *Hyla*, *Leptodactylus* ou talvez *Eleutherodactylus*).

Material examinado: tabela.

Tabela 4 — *Chironius carinatus*

Chironius flavolineatus (Boettger)

Herpetodryas flavolineatus Boettger, 1885:234. Localidade típica: Paraguai.

Chironius flavolineatus; Bailey, 1955, 571:13; Peters & Orejas-Miranda, 1970, 297:60; Cordeiro & Hoge, 1973:266.

Diagnose — Nasal dividido; loreal mais longa que alta; órbita com diâmetro maior que sua distância da narina; 1 pré e 2 postoculares, às vezes 3; temporais 1+1; supralabiais 9-9 (4.^o, 5.^o e 6.^o tocando a órbita); infralabiais 10-10 (5 em contato com a mental anterior); mentais anteriores mais curtos que os posteriores. Escamas dorsais em 12-12-10 séries longitudinais fortemente oblíquas, com duas linhas carenadas vertebrais pouco acentuadas, mais fracas nas fêmeas; fossetas apiculares presentes na região nugal e pescoço. Anal dividida. Dentes maxilares 33-41. Ventrals 151-154, caudais 140 (em um exemplar macho completo). Comprimento total do exemplar citado, n.^o 84, 842 mm (corpo 510 mm e cauda 332 mm).

Colorido em preservativo: Nos dois espécimes conservados nesta Seção o colorido desvaneceu-se em grande parte, permanecendo apenas de forma evidente a faixa vertebral amarelada brilhante, que se estende da nuca até a metade do corpo; marginando esta faixa desde os lados do pescoço até o meio do corpo e às ventrais uma tonalidade cinza escura. Superfície ventral amarelada. Na cabeça, a parte superior pardo escura e os supralabiais amarelos.

Comentários — Esta é a primeira vez que se refere a ocorrência desta espécie na área de floresta Amazônica. Bailey (1955:15) analisou exemplares da Bahia, S. Paulo, Goiás (Goiânia) e Mato Grosso; Peters & Orejas-Miranda (1970:60) além das áreas já citadas, referem ainda Paraguai e Bolívia Central; por fim Cordeiro & Hoge (1973:266), localizaram a espécie em Pernambuco.

Os dois espécimes aqui estudados procedem do sul do Pará, sendo o de n.^o 84 da Serra Norte (região da Serra dos Carajás, município de Marabá) e o de n.^o 230 da Serra do Cachimbo, (base aérea da Aeronáutica — FAB), região oeste do Estado, limite com Mato Grosso. É interessante observar que *C. flavolineatus* vive em áreas de vegetação aberta (cerrado ou campo cerrado). No Pará ocorrem manchas de cerrado típico, especialmente na região sul e mais acentuadamente no topo de algumas chapadas, que não apresentam mais que 600 a 700 metros de altitude, como as de Carajás e Cachimbo. Um dos autores (Cunha) visitou em maio de 1969 a Serra Norte (Carajás) onde coletou o espécime n.^o 84 e exemplares de outras espécies de ofídios e lagartos. Algumas observações foram depois publicadas em trabalho (Cunha, 1970) abordando o ambiente da região.

Os exemplares do sul do Pará ajustam-se bem aos caracteres apresentados por Bailey (1955:4-8 e 13), dentre os quais citamos: 1 temporal, posterior usualmente; 9 supralabiais, dos quais o 4.^o, 5.^o e 6.^o tocando

a órbita; dentes maxilares 33-41 (em Bailey encontra-se 32-38); uma distinta faixa amarela brilhante vertebral até o meio do corpo, marginada por duas filas de escamas carenadas. Alimenta-se de rãs (*Hyla?*) de acordo com o exame do conteúdo estomacal.

Material examinado — Tabela 5

Chironius multiventris Schmidt & Walker

Chironius multiventris Schmidt & Walker, 1943:282. Localidade típica: Departamento de Madre de Dios, Peru.

Chironius multiventris; Hoge, 1964:54; Dixon & Soini, 1977:40.

Chironius cochranæ Hoge & Romano, 1969:93. Localidade típica: Utinga, Belém, Pará; Cunha & Nascimento, 1978:63.

Diagnose — Nasal dividida; loreal mais longa que larga; órbita com diâmetro maior que sua distância da narina; 1 pré e 3 postoculares freqüentemente, porém quase freqüente 1+2, às vezes 1+2 de um lado e 1+3 de outro ou 1+3 de um lado e 1+4 de outro, mais raramente 1+4 de ambos os lados; temporais usualmente 1+2, raramente 1+1; supra-labiais normalmente 9-9, às vezes 8-8; 9-10, 10-10 raramente (4.^o, 5.^o e 6.^o usualmente tocando a órbita, raramente 5.^o e 6.^o ou 5.^o, 6.^o e 7.^o); infralabiais freqüentemente 10-10, às vezes 9-9, 9-10, 10-11 e 11-11 (normalmente 5 em contato com o mental anterior, raramente 6 ou 5-6); mentais anteriores mais curtas que as posteriores. Escamas dorsais usualmente em 12-12-10 séries longitudinais (alguns exemplares em 12-12-8, 12-12-9, 13-12-10 e 14-12-10), com duas filas vertebrais carenadas, fortemente nos machos e nas fêmeas débeis; as escamas laterais acentuadamente oblíquas, excetuando as paraventrals; fossetas apiculares presentes em todas as escamas do corpo, usualmente até às proximidades da região anal, mais freqüentes na nuca e pescoço, em geral uma, mais raramente duas fossetas em cada escama. Anal dividida. Dentes maxilares 34-38. Ventrals 184 a 193 nos machos e nas fêmeas 183 a 193; caudais divididas, 189 a 203 nos machos e nas fêmeas 192 a 201 (excepcionalmente encontramos uma fêmea com 206 caudais, que evidentemente extrapola do comum). Comprimento do maior exemplar com cauda completa, n.^o 12.928 fêmea, do lugar Colônia Nova, BR-316 próximo ao rio Gurupí, Pará, corpo 1.213 mm e cauda 762 mm, total 1.975 mm.

Colorido fundamental do corpo e cauda pardo oliváceo; cabeça mais clara com a região látero-nucal mais acentuada insinuando esboço de um colar; em muitos exemplares machos encontra-se a faixa clara vertebral marginada de pardo escuro, que tem início no pescoço e se estende em grande parte do corpo e parte anterior da cauda; na parte pósterolateral do corpo e cauda, barras claras transversas, espaçadas umas das outras; o pardo escuro dos lados do corpo normalmente se estendendo às laterais das ventrais e caudais, às vezes formando uma faixa mais enegrecida na cauda. Ventrals fortemente anguladas, amarelo esbranquiçado, mostrando uma linha escurecida, na região mediana, inclusive na inserção das caudais. Jovens com barras transversais claras em zigzague, mais acentuadas que os adultos.

Comentários — Esta espécie, descrita por Schmidt & Walker (1943: 282) em dois espécimes do Peru, ficou perfeitamente caracterizada, por possuir ventrais e caudais muito elevadas, em relação às outras *Chironius*,

TABELA 4
Chironius carinatus — Maranhão

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrais	Anal	Subcaud.	Sup. Labial	Infr. Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anal	Coltor
10.867	São Raimundo - BR-316	11/75	♀	12-12-10	159	1/1	118/118	8/9	11/10	33.5	89.0	41.0		1+2	1+2		Cunha & Nascimento
13.594	Gancho do Arari	10/77	♀	12-12-10	159	1/1	—	8/8	10/10	34.0	89.0	—		1+2	1+2		Nascimento
13.595	Gancho do Arari	10/77	♀	12-12-8	163	1/1	—	8/8	10/10	42.0	1.070	—		1+2	1+2		Nascimento
13.596	Gancho do Arari	10/77	♀	12-12-10	154	1/1	124/124	9/9	11/11	44.3	1.087	56.0		1+3 1+2	1+1 1+2		Nascimento
13.597	Gancho do Arari	10/77	♂	12-12-8	184	1/1	123/123	8/8	9/10	37.4	94.5	46.0		1+2	1+2		Nascimento
14.295	Gancho do Arari	02/78	♂	14-12-10	154	1/1	—	8/8	10/10	43.0	1.120	—		1+2	1+2		Cunha & Nascimento
14.643	Gancho do Arari	07/78	♀	12-12-10	158	1/1	—	8/8	10/10	39.4	1.060	—		1+2	1+2		Cunha & Nascimento
14.647	Gancho do Arari	07/78	♂	12-12-10	156	1/1	—	8/8	10/10	41.0	1.134	—		1+2	1+2		Cunha & Nascimento
14.648	Gancho do Arari	07/78	♂	12-12-10	154	1/1	—	8/8	9/9	42.3	1.060	—		1+2	1+2		Cunha & Nascimento
14.650	Gancho do Arari	07/78	♂	12-12-10	154	1/1	—	8/8	10/10	44.3	1.095	—		1+2	1+2		Cunha & Nascimento
14.651	Gancho do Arari	07/78	♀	12-12-8	155	1/1	—	8/8	11/11	42.0	1.060	—		1+2	1+2		Cunha & Nascimento
14.652	Gancho do Arari	07/78	♀	12-12-10	161	1/1	117/117	9/9	11/11	42.4	1.130	62.5		1+2	1+2		Cunha & Nascimento
14.653	Gancho do Arari	07/78	♂	12-12-10	158	1/1	122/122	9/9	10/10	40.0	1.090	53.0		1+2	1+2		Cunha & Nascimento
14.654	Gancho do Arari	07/79	♀	12-12-10	150	1/1	—	9/9	11/11	41.0	1.090	—		1+2	1+2		Cunha & Nascimento
14.655	Gancho do Arari	07/78	♂	12-12-10	153	1/1	115/116	8/8	11/11	38.5	96.0	49.5		1+2	1+2		Cunha & Nascimento
14.656	Vitória do Meirim	07/78	♂	12-12-10	156	1/1	—	8/8	10/10	36.8	86.5	—		1+2	1+2		Cunha & Nascimento
15.586	Gancho do Arari	08/79	♂	12-12-10	156	1/1	—	9/9	10/11	45.0	1.183	—		1+2	1+2		Nascimento & Reigalido
15.587	Gancho do Arari	08/79	♂	12-12-10	153	1/1	122/122	8/8	10/10	44.0	1.145	58.4		1+2	1+2		Nascimento & Reigalido
15.588	Gancho do Arari	08/79	♂	12-12-10	155	1/1	120/120	8/8	10/10	42.0	1.215	60.0		1+2	1+2		Nascimento & Reigalido
15.589	Gancho do Arari	08/79	♂	12-12-10	155	1/1	121/121	8/9	10/10	41.9	1.084	54.5		1+2	1+2		Nascimento & Reigalido
15.590	Gancho do Arari	08/79	♂	12-12-10	154	1/1	118/118	8/8	10/10	43.0	1.030	51.5		1+2	1+2		Nascimento & Reigalido
15.591	Gancho do Arari	08/79	♂	12-12-10	153	1/1	—	8/9	10/11	46.5	1.215	—		1+2	1+2		Nascimento & Reigalido
15.592	Gancho do Arari	08/79	♀	14-12-10	150	1/1	116/116	8/8	11/10	40.0	1.066	49.5		1+2	1+2		Nascimento & Reigalido
15.593	Gancho do Arari	08/79	♂	12-12-10	158	1/1	—	8/8	10/10	38.7	1.042	—		1+2	1+2		Nascimento & Reigalido

TABELA 4 (cont.)
Chironius carinatus — Maranhão

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anal	Coletor
15.584	Gancho de Arari	08/79	♂	14-12-10	130	1/1	—	8/8	10/10	27.0	616	—	—	1+2	1+2	—	Nascimento & Resignado
15.591	Gancho de Arari	08/79	♂	12-12-10	153	1/1	—	8/8	10/10	37.7	1.073	—	—	1+2	1+2	—	Nascimento & Resignado
15.602	Gancho de Arari	08/79	♂	14-12-10	162	1/1	123/123	8/8	10/10	36.0	995	405	—	1+2	1+2	—	Nascimento & Resignado
15.603	Gancho de Arari	08/79	♂	12-12-10	156	1/1	—	8/9	10/11	43.0	1.180	—	—	1+2	1+2	—	Nascimento & Resignado
15.611	Gancho de Arari	08/79	♂	12-12-10	155	1/1	117/117	9/9	10/10	29.0	758	190	—	1+2	1+2	—	Nascimento & Resignado

Chironius carinatus — Pará

646	Illa de Mosquero	06/71	♂	12-12-10	159	1/1	133/133	9/9	10/10	41.0	1.304	620	—	1+2	1+2	—	Cunha & Nascimento
8.066	Fazenda Vencedora Arari-Mantijó	03/75	♀	13-12-10	162	1/1	—	8/9	10/10	34.0	1.069	—	—	1+2	1+2	—	Moreira
14.291	Ipitanga — Estrada Acari-Moju	02/76	♀	12-12-10	158	1/1	—	9/9	11/10	40.0	968	—	—	1+2	1+2	—	Cunha & Nascimento

Chironius carinatus — Roraima

483	Colônia — Coronel Meia	06/70	♂	12-12-9	160	1/1	132/132	9/9	11/11	23.0	670	374	—	1+2	1+2	—	Nascimento
485	Colônia — Coronel Meia	06/70	♂	12-12-9	160	1/1	—	9/9	10/11	35.5	850	—	—	1+2	1+2	—	Nascimento
488	Colônia — Coronel Meia	06/70	♂	12-12-9	158	1/1	—	8/8	10/10	39.4	967	483	—	1+2	1+2	—	Nascimento

Chironius carinatus — Amapá

69	Macapá	06/69	♀	14-12-10	160	1/1	124/124	9/9	11/11	23.7	632	315	—	1+2	1+2	1+3	Reimundo Vasconcelos
438	Macapá	11/69	♂	12-12-3	152	1/1	124/124	9/9	11/11	43.0	1.010	510	—	1+2	1+2	—	Nascimento

Chironius carinatus — Amazonas

146	Rio Javari Estirão do Equador	11/60	♂	12-12-10	150	1/1	—	9/9	10/10	27.7	824	—	—	1+2	1+2	—	Hidai
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TABELA 5
Chironius Flavivestitus — Pará

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anal	Coletor
84	Serra da Carajás (Serra Negra)	06/69	♂	12-12-10	154	1/1	140/140	9/9	10/10	18.9	510	332	—	1+3	1+1	—	Cunha
230	Serra do Cachimbo	01/62	♀	12-12-10	151	1/1	—	9/9	10/10	22.0	601	—	—	1+2	1+1	—	João Hidai

e coloração conspícua, ainda que variável dentro de uma mesma população ou de populações afastadas. Hoge (1964:54) identificou um exemplar de Suriname como *C. multiventris*, de fato com os caracteres desta espécie com pequenas variações de coloração.

Depois, Hoge & Romano (1969:93) resolveram descrever *C. cochranac* como nova tendo por tipo um exemplar de Utinga, Belém, Pará e por parátipos o citado espécime e mais outro de Suriname, além de sete exemplares da Guiana. Os mesmos autores acentuaram que a nova espécie se diferenciaria pela ausência de faixa clara vertebral, ausência de margem escura nas ventrais e caudais, cor escura dorsal cobrindo as bordas ventrais e caudais em todo o corpo e bem como indistintas faixas transversais claras dos lados não orlando-as de negro.

Cunha & Nascimento (1978:63) seguindo em grande parte Hoge & Romano (id.) identificaram 28 exemplares do leste do Pará como *C. cochranac* pelo fato de alguns apresentarem estes caracteres. Porém depois examinando mais exemplares com a descrição original de *C. multiventris* Schmidt & Walker e o trabalho de Dixon & Soini (1977:40) sobre os ofídios da região de Iquitos, Peru, foi possível chegarmos a conclusão diferente pois *C. cochranac* é apenas um sinônimo de *C. multiventris*. Estes últimos autores já haviam concluído por este novo status. Foram examinados 75 indivíduos de várias procedências do Pará, Amapá e Maranhão, nos quais procuramos avaliar os caracteres mais freqüentes e medir as variações individuais dentro de uma população e entre populações afastadas, comparando dados obtidos por Hoge & Romano (1969) e Dixon & Soini (1977). Podemos pois concluir que não existem diferenças entre *C. cochranac* e *C. multiventris*.

A espécie é relativamente freqüente no Pará, porém pouco comum no Maranhão. Quanto ao Amapá ainda persiste deficiência de coletas. Tem sido encontrada na floresta primária, capoeiras e roçados. Conforme a análise do conteúdo estomacal, alimenta-se especialmente de pequenos anfíbios (rãs dos gêneros *Hyla*, *Eleutherodactylus* e *Leptodactylus*) e às vezes de lagartos (*Anolis fuscoauratus* d' Orbigny, 1863), *Polychrus marmoratus* (Linnaeus, 1758) e *Tropidurus torquatus hispidus* (Spix, 1825).

Material examinado: 75 espécimes.

Tabela 6

ABSTRACT: Snakes of the Amazon Basin. XV. The species of *Chironius* from the eastern Amazon Basin (Pará, Amapá and Maranhão). (Ophidia: Colubridae). Throughout much of Brazil and particularly in the Amazonian Region the species of *Chironius* are little-known and imperfectly studied. Some 379 specimens of this genus were brought together for a reevaluation of the species which occur in the eastern Amazon Basin, including the States of Pará and Maranhão and the Federal Territory of Amapá. The species are redefined through comparative analysis and contrasted with published descriptions. The following species are considered to be valid: *Chironius carinatus*, *C. exoletus*, *C. scurrulus*, *C. fuscus* (previously confused with *Natrix cinnamomea* Wagler), *C. multiventris* (previously misidentified as *C. cochranac* Hoge & Romano), and *C. flavolineatus* (which is reported for the first time for the Amazon Basin, being found from the "cerrado" scrub forest of eastern and central Brazil to the State of Mato Grosso and Paraguay).

TADELA 6
Chironius multiventris — Amapá

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infr. Labial	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Auel	Coior	
330	Serra do Navio	10/68	♀	14-12-10	190	1/1	—	9/9	10/10	32.0	1.010	—	—	1+3	1+2	—	Paulo Ebbwhein	
334	Rio Traçajuba	07/69	♂	12-12-10	186	1/1	—	9/9	10/10	36.5	1.215	—	—	1+3	1+2	—	Nascimento	
Chironius multiventris — Maranhão																		
10.221	Nova Vida	06/75	♀	14-12-10	188	1/1	197/198	9/9	10/10	27.8	850	586	—	1+2	1+2	—	Cunha & Rosemro	
10.431	Paraná	10/76	♂	12-12-10	190	1/1	—	9/10	10/10	42.5	1.410	—	—	1+2	1+2	—	Nascimento	
11.069	Nova Vida	02/78	♂	12-12-8	192	1/1	203/202	9/9	10/10	23.0	915	550	—	1+3	1+2	—	Cunha & Nascimento	
11.154	Nova Vida	02/76	♀	12-12-10	189	1/1	199/199	9/9	10/10	37.0	1.191	758	—	1+3	1+2	—	Cunha & Nascimento	
12.730	Nova Vida	10/76	♂	12-12-10	189	1/1	—	9/9	10/10	38.0	1.289	—	—	1+2	1+1	—	Cunha & Nascimento	

Chironius multiventris — Pará

33	Pará		♂	12-12-9	190	1/1	—	9/9	11/11	39.0	1.300	—	—	1+3	1+2	—	—
368	APEG — Belém	1965	♂	12-12-10	191	1/1	—	9/9	11/10	30.4	1.002	—	—	1+2	1+2	—	—
369	APEG — Belém	1965	♀	12-12-10	186	1/1	—	9/9	10/10	27.0	860	—	—	1+2	1+2	—	—
556	Iha de Mosqueiro	09/71	♀	12-12-10	193	1/1	201/201	9/9	10/10	25.4	810	545	—	1+3	1+2	—	Millon Gonçalves
740	Km 4 da Estrada Altemira-Iatuba	07/71	♂	12-12-10	188	1/1	—	9/9	10/10	33.3	1.220	—	—	1+3	1+2	—	Nascimento
1.114	Santa Bárbara	02/72	♂	12-12-10	190	1/1	184/194	9/9	10/10	25.7	875	540	—	1+3	1+2	—	Barata
1.183	Santo Antonio do Teuçá	03/72	♀	12-12-10	188	1/1	—	9/9	9/10	23.5	865	—	—	1+2	1+2	—	Cunha & Nascimento
1.548	Bom Vista	06/72	♂	12-12-10	187	1/1	—	9/9	11/11	36.0	1.110	—	—	1+3	1+2	—	Cunha & Nascimento
1.897	Peixe-Boi	06/72	♂	12-12-10	188	1/1	—	9/9	10/11	31.0	855	—	—	1+2	1+2	—	Cunha & Nascimento
2.168	Limão Grande	09/72	♀	12-12-10	188	1/1	—	9/9	11/11	37.4	1.196	—	—	1+3	1+2	—	Cunha & Barata
2.260	Bela Vista	09/72	♀	12-12-10	191	1/1	—	9/9	11/11	33.5	1.077	—	—	1+3	1+2	—	Cunha & Nascimento
2.743	Km 23 da Estrada de Maracanã	03/73	♂	12-12-10	190	1/1	—	9/9	11/11	43.0	1.365	—	—	1+3	1+2	—	Cunha & Nascimento
2.769	Km 63 da Estrada de Maracanã	03/73	♂	12-12-10	192	1/1	—	10/10	10/11	43.0	1.369	—	—	1+3	1+2	—	Cunha & Nascimento
3.065	Bela Vista	03/73	♂	12-12-10	186	1/1	—	9/9	10/11	41.7	1.385	—	—	1+3	1+2	—	Cunha & Nascimento
3.239	Santa Bárbara	06/73	♀	12-12-10	191	1/1	192/192	9/9	10/10	16.0	355	223	—	1+3	1+2	—	Cunha & Nascimento
3.384	Km 23 da Estrada de Maracanã	06/73	♂	14-12-10	188	1/1	—	9/9	10/10	42.0	1.265	—	—	1+3	1+2	—	Cunha & Nascimento
3.706	Bela Vista	06/73	♂	13-12-10	185	1/1	190/190	9/9	-10/10	21.6	636	386	—	1+3	1+2	—	Cunha & Nascimento
3.907	Peixe-Boi	06/73	♀	12-12-10	191	1/1	—	9/9	11/11	41.0	1.340	—	—	1+2	1+2	—	Cunha & Nascimento

TABELA 6 (cont.)
Chironius multivestris - Pará

N.º	PROCEDÊNCIA	Data	Sexo	Dorsais	Ventrais	Anal	Súbdod.	Sup. Labial	Infra-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anel	Cordeir
3.929	Santa Rosa	05/73	♂	12-12-10	187	1/1	—	9/9	11/11	31.0	983	—	1+2	1+2	1+2	—	Cunha & Nascimento
4.046	Bom Jesus	07/73	♀	12-12-10	189	1/1	—	9/9	10/10	30.6	980	—	1+3	1+2	1+2	—	Cunha & Nascimento
4.726	Santo Antonio do Tauá	10/73	♀	12-12-10	190	1/1	—	9/9	11/11	30.0	1.035	—	1+2	1+2	1+2	—	Cunha & Nascimento
5.787	Bom Jesus	03/74	♂	12-12-10	184	1/1	—	9/9	10/10	37.6	1.180	—	1+3	1+2	1+2	—	Cunha & Nascimento
5.777	Bom Jesus	03/74	♂	12-12-10	187	1/1	189/189	9/9	10/10	37.4	1.186	725	1+3	1+2	1+2	—	Cunha & Barata
5.859	Macapaíno	03/74	♂	12-12-10	191	1/1	—	9/10	11/11	36.0	1.200	—	1+2	1+2	1+2	—	Cunha & Barata
5.895	Mirauá	03/74	♂	12-12-10	186	1/1	—	9/9	10/10	34.6	1.170	—	1+3	1+2	1+2	—	Cunha & Barata
5.926	Trombetinha	03/74	♂	12-12-10	187	1/1	—	9/9	10/10	31.0	1.010	—	1+4	1+2	1+2	—	Cunha & Barata
6.950	Jupiaúba	07/74	♂	12-12-10	186	1/1	—	9/9	11/11	37.0	1.300	—	1+3	1+2	1+2	—	Cunha & Nascimento
7.090	Mirauá	03/74	♂	12-12-10	187	1/1	—	9/9	11/11	38.0	1.245	—	1+2	1+1	1+1	—	Cunha & Nascimento
7.159	Macapaíno	07/74	♂	12-12-8	187	1/1	—	8/8	10/10	32.0	1.045	—	1+3	1+2	1+2	—	Cunha & Nascimento
7.160	Macapaíno	07/74	♂	12-12-10	190	1/1	—	9/9	11/11	35.0	1.090	—	1+2	1+2	1+2	—	Cunha & Nascimento
7.344	Bom Jesus	07/74	♂	12-12-10	191	1/1	200/200	9/9	10/10	23.0	703	465	1+3	1+2	1+2	—	Cunha & Nascimento
7.365	Bom Jesus	07/74	♂	13-12-10	191	1/1	—	9/9	10/10	38.0	1.325	—	1+2	1+2	1+2	—	Cunha & Nascimento
7.708	Santa Rosa	07/74	♂	12-12-10	192	1/1	195/195	9/9	11/11	26.7	835	520	1+3	1+4	1+2	—	Cunha & Nascimento
8.279	Bom Jesus	10/74	♂	12-12-10	186	1/1	—	9/9	10/10	24.0	777	—	1+2	1+2	1+2	—	Nascimento
8.407	Pratinha	07/74	♀	12-12-10	188	1/1	—	9/9	10/10	35.6	1.305	—	1+2	1+2	1+2	—	Cunha & Nascimento
8.411	Pratinha	07/74	♀	12-12-10	188	1/1	—	9/9	11/8	25.8	890	—	1+3	1+2	1+2	—	Cunha & Nascimento
8.602	Pratinha	02/75	♀	12-12-10	190	1/1	197/197	9/9	10/10	16.3	316	225	1+2	1+2	1+2	—	Cunha & Nascimento
8.656	Macapaíno	02/75	♀	12-12-10	187	1/1	—	9/9	10/10	34.0	1.070	—	1+3	1+2	1+2	—	Cunha & Nascimento
8.672	Km 16 da Estrada do Acriá	02/75	♀	12-12-10	186	1/1	195/195	8/8	10/10	22.0	585	345	1+2	1+2	1+2	—	Cunha & Nascimento
9.205	Santa Rosa	02/75	♂	12-12-9	191	1/1	—	9/9	10/11	39.3	1.270	—	1+2	1+2	1+2	—	Cunha & Nascimento
9.207	Santa Rosa	02/75	♀	12-12-10	192	1/1	—	9/9	11/11	33.5	1.120	—	1+2	1+2	1+2	—	Cunha & Nascimento
9.208	Santa Rosa	02/75	♀	12-12-10	191	1/1	—	9/9	10/10	33.4	1.064	—	1+4	1+2	1+2	—	Cunha & Nascimento
9.229	Santa Rosa	06/75	♀	14-12-10	187	1/1	—	9/9	10/10	31.4	1.010	—	1+3	1+2	1+2	—	Cunha & Roseiro
9.359	Km 16 da Estrada do Acriá	06/75	♂	12-12-10	190	1/1	—	9/9	10/10	42.0	1.345	—	1+3	1+2	1+2	—	Cunha & Nascimento

TABELA 6 (cont.)
Chironius multiventris — Pará

N.º	PROCEDENCIA	Data	Sexo	Dorsais	Ventrals	Anal	Subcaud.	Sup. Labial	Infr.-Lab.	C. Cabeça em mm	C. Corpo em mm	C. Cauda em mm	Dentição	Ocular	Temp.	Anel	Color
9.410	Igarapé — Pirajuará	06/75	♂	12-12-10	185	1/1	—	9/9	10/10	41.0	1.334	—	—	1+2 1+2	1+2		Cunha & Rosemire
9.453	Boa Vista	06/75	♀	12-12-10	188	1/1	—	9/9	10/10	37.0	1.210	—	—	1+3	1+2		Cunha & Rosemire
9.467	Macapatinho	06/75	♂	12-12-10	193	1/1	—	9/9	10/10	37.0	1.251	—	—	1+3	1+2		Cunha & Nascimento
9.526	Santa Luzia	06/75	♂	12-12-10	188	1/1	195/195	9/9	10/10	26.6	860	665	—	1+3	1+2		Cunha & Rosemire
9.527	Santa Luzia	06/75	♂	12-12-8	186	1/1	—	9/9	10/10	37.7	1.192	—	—	1+3	1+2		Cunha & Rosemire
10.069	Curupati	06/75	♂	12-12-10	192	1/1	199/199	9/9	10/10	29.6	770	488	—	1+2	1+2		Cunha & Rosemire
10.625	Boa Vista	11/75	♂	12-12-10	190	1/1	—	9/9	11/11	35.7	1.128	—	—	1+2 1+3	1+2		Cunha & Nascimento
11.145	Vila Nova	06/76	♂	12-10	184	1/1	—	9/9	10/10	43.2	1.493	—	—	1+2	1+2		Cunha & Nascimento
11.160	Km 11 da PA-332	07/76	♂	12-12-6	187	1/1	182/192	8/8	9/9	30.0	904	696	—	1+3	1+2		Cunha & Nascimento
11.802	Macapatinho	06/76	♀	12-12-10	192	1/1	—	9/9	10/10	31.0	1.065	—	—	1+3 1+4	1+2		Cunha & Nascimento
11.860	Pratinha	05/76	♂	12-12-10	188	1/1	—	9/9	10/10	32.0	1.036	—	—	1+3 1+4	1+2		Cunha & Nascimento
11.866	Santa Rosa	05/76	♀	12-12-10	192	1/1	206/206	9/9	10/10	37.7	1.025	685	—	1+4	1+2		Cunha & Nascimento
11.868	Santa Rosa	05/76	♂	12-12-10	188	1/1	—	9/9	10/10	40.7	1.245	—	—	1+3 1+2	1+2		Cunha & Nascimento
11.869	Santa Rosa	05/76	♂	12-12-10	192	1/1	—	9/9	10/10	34.0	1.245	—	—	1+2	1+2		Cunha & Nascimento
11.870	Santa Rosa	05/76	♀	12-12-10	189	1/1	—	9/9	10/10	32.6	1.022	—	—	1+2	1+2		Cunha & Nascimento
12.006	Colônia Nova	06/76	♀	12-12-10	190	1/1	192/191	9/9	10/10	27.0	847	547	—	1+2	1+2		Cunha & Nascimento
12.166	São Pedro — Capitão Poço	06/76	♂	12-12-10	184	1/1	—	9/9	10/10	30.0	980	—	—	1+2	1+2		Cunha & Nascimento
12.188	São Pedro — Capitão Poço	06/76	♀	14-12-10	183	1/1	—	9/9	11/11	37.0	1.165	—	—	1+3 1+2	1+2		Cunha & Nascimento
12.262	Bom Jesus	06/76	♀	12-12-10	187	1/1	180/193	9/9	10/10	35.4	1.063	695	—	1+3 1+2	1+2		Cunha & Nascimento
12.263	Bom Jesus	06/76	♂	12-12-10	187	1/1	—	9/9	10/10	35.0	1.055	—	—	1+2	1+2		Cunha & Nascimento
12.576	Pratinha	06/76	♂	12-12-8	189	1/1	—	9/9	10/11	42.0	1.340	—	—	1+4	1+2		Cunha & Nascimento
12.580	Santa Rosa	09/76	♂	14-12-10	190	1/1	200/200	9/9	10/10	27.0	900	587	—	1+2 1+2	1+2		Cunha & Nascimento
12.598	Colônia Nova	10/76	♀	14-12-10	191	1/1	192/192	9/9	10/10	35.5	1.213	762	—	1+2	1+2		Cunha & Nascimento
13.005	PA-332 Sítio Bela Vista	10/77	♂	12-12-10	191	1/1	—	9/9	10/10	41.4	1.375	—	—	1+3	1+2		Nascimento
16.357	Sítio Rajmundo Agroindustrial - (Jari)	09/80	♀	12-12-10	193	1/1	190/190	9/9	10/9	29.0	860	626	—	1+2	1+2		Nascimento & Reinaldo

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FAUNA DE SERPENTES DA PROVÍNCIA PAMPEANA E INTER-RELAÇÕES COM AS PROVÍNCIAS LÍMITROFES

Thales de LEMA *

RESUMO: A Província Zoogeográfica Pampeana situa-se desde as terras baixas do Rio Grande do Sul, Brasil e do nordeste da Argentina, até o Uruguai e as Províncias políticas argentinas de Buenos Aires e leste de La Pampa. Há dois Centros de Dispersão evidentes: o Bonariense e o Uruguaio. O Bonariense fornece ofiofauna para a mesopotâmia dos rios Uruguai e Paraná, a nordeste da Argentina. É o Uruguaio para o Rio Grande do Sul, inclusive as encostas e margens do Planalto Meridional do Brasil. Pelo Planalto chega fauna do Centro Paranense (Província Guarani) e, pelo litoral florestado, do Centro da Serra do Mar (Província Tupi). Em menor escala, chega fauna da Província Bororo, do oeste, principalmente da bacia do Paraná superior. Essas ofiofaunas se encontram ao norte do Rio Grande do Sul e da Argentina configurando uma região transicional entre duas grandes sub-regiões, a Guiano-brasileira e a Andino-patagônica. É formulada uma hipótese sobre a história da dispersão da ofiofauna pampeana, com base nos padrões de variação de diversas espécies e zonas de intergradação de subespécies.

INTRODUÇÃO

Durante muitos anos estudando serpentes do Estado do Rio Grande do Sul e regiões adjacentes do Uruguai e Argentina, principalmente, temos notado uma certa gradação geográfica na variação das espécies que são próprias da Província Pampeana.

Analisando a variação em determinadas espécies como *Elapomorphus bilineatus*, *Lystrophis dorbignyi*, *Leimadophis poecilogyrus*, *Philodryas sestivus*, e outras, chegamos a algumas conclusões dignas de nota e que expomos aqui, mas, com a ressalva de que, uma conclusão final só será possível quando as principais espécies da área forem analisadas.

A bibliografia específica para a área conta, principalmente, com os artigos de Hensel (1868)¹⁹, Boulenger (1885a)⁸, (1885b)⁹, (1886)¹⁰, Cope (1885)¹³, Lema & Fabián-Beurmann (1977)²⁸ e Lema *et alii* (1980)³⁰ — para o Rio Grande do Sul. Para o Uruguai, destaca-se Devincenzi (1925)¹⁴

* Museu de Ciências Naturais da Fundação Zoológica do Rio Grande do Sul. Bolsista do CNPq (Proc. IIII — 690/76). Caixa Postal 1188, 90.000 Porto Alegre, RS, Brasil.

e Vaz-Ferreira & Soriano (1960)³⁷. Para a Argentina, Koslowsky (1898)²² e Abalos & Mischis (1975)¹. Para o Paraguai, Bertoni (1939)⁷. Para o Brasil em geral, atingindo o extremo-sul, destacam-se: Amaral (1929)⁴, (1936)⁵ (1977)⁶; Peters & Orejas-Miranda (1970)³⁵, Hoge (1965)²⁰ e Hoge, Cordeiro e Romano (1975)²¹.

Para a apreciação zoogeográfica foram levados em conta os estudos de Fittkau (1969)¹⁵, Lema (1971)²⁵ e Müller (1973)³⁴.

O material que serviu de base para este trabalho está depositado nas coleções do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brasil; Instituto Butantan de São Paulo, Brasil; Museo Nacional de História Natural de Montevideo, Uruguai; Museo Argentino de Ciencias Naturales de Buenos Aires, Argentina; Museo de História Natural de Paraná, Entre Ríos, Argentina.

ÁREA FÍSICA E POLÍTICA

A área geográfica da Província Pampeana do ponto de vista da ofiofauna, compreende as terras baixas do Estado do Rio Grande do Sul (a maior parte desse Estado) e que seguem para o Uruguai e Província de Buenos Aires, Argentina — pelo leste. Pelo centro, estende-se do Rio Grande do Sul para oeste, na mesopotâmia formada pelos rios Paraná e Uruguai: a parte não florestada da Província de Misiones e as Províncias de Corrientes e Entre Ríos.

Fisionomicamente essa área apresenta-se, de um modo geral, plana com algumas ondulações (coxilhas) e elevações (serras) baixas. Ao norte do Rio Grande do Sul, a Província Pampeana é limitada pelas bordas do Planalto Meridional do Brasil, cujas cotas vão baixando de leste a oeste, chegando ao nível do mar nas margens do rio Uruguai (Vale do Uruguai). Ao norte de Misiones, há a Serra de Misiones que é florestada — essa florestal é subtropical e estende-se do Paraguai meridional para o noroeste do Rio Grande do Sul, oeste do Estado de Santa Catarina e sudoeste do Estado do Paraná (Brasil): A sudeste do Rio Grande do Sul há elevações (Serra do Sudeste) destacando-se a Serra dos Tapes e a do Herval e que seguem para o sul até a região de Maldonado, no Uruguai, onde a altitude média é de 500 m. Na região da Província Brasil-Uruguai há elevações baixas e o pampa do Uruguai é um pouco mais alto que o da Argentina. Neste país há elevações apenas ao sul de Buenos Aires (Sierra de la Ventana e Sierras de Tándil). O pampa é todo gramado, mas a vegetação empobrece de norte a sul e de leste a oeste, o mesmo se nota quanto à fauna em geral e à ofiofauna. O litoral do extremo sul de Santa Catarina até Buenos Aires é baixo e arenoso, com dunas, havendo rochedos isolados em pequenos grupos em alguns pontos como Torres (Rio Grande do Sul), Isla de Lobos (Montevideo) etc. Junto ao litoral dessa área, há numa rede de lagoas, algumas gigantes como a Lagoa dos Patos (Rio Grande do Sul) e a Mirim (Brasil-Uruguai).

As barreiras observadas para a dispersão da ofiofauna pampeana foram: os cursos inferiores dos rios Paraná e Uruguai, isolando a parte sul da mesopotâmia argentina de Buenos Aires e do Uruguai. O Río de La Plata, isolando Buenos Aires do Uruguai. Os desertos a noroeste e

sul da Argentina, principalmente o da Patagônia. A oeste da Argentina, zona pedregosa e que antecede a Cordilheira dos Andes, é barreira para a ofiofauna. Não vimos fauna pampeana na estreita área de terras baixas junto ao litoral atlântico, ao sul de Buenos Aires, mas, sim ofiofauna subandina. (Fig. 1)

OS CENTROS DE DISPERSÃO

Com base em Fittkau¹⁵ e Müller³⁴ e no material examinado, notamos, pelo menos, dois Centros de Dispersão de ofiofauna pampeana: o Bonariense e o Uruguaio.

O *Centro de Dispersão Bonariense* situa-se na Província de Buenos Aires. A dispersão deu-se para todos os lados, ocupando toda a Província e, para o sul é barrada pela Patagônia; para oeste chega a atingir nitidamente o lado leste da Província de La Pampa; mais para oeste diminui e desaparece a fauna pampeana, onde surgem as elevações da pré-cordilheira; aí predomina fauna subandina, diferenciada da pampeana; pela vegetação mais rica do delta do rio Paraná pela margem direita do mesmo, dispersa-se a fauna bonariense em direção ao norte; evita o lado oeste, árido e o noroeste, desértico, bem como a região do Chaco e povoa a mesopotâmia pelo norte, através do Paraná médio. A mesopotâmia é uma savana úmida e rica. Algumas poucas formas penetram no Uruguai por sua área extrema noroeste, bem como no Rio Grande do Sul, cruzando o rio Uruguai, que não é barreira física suficiente para répteis em geral. Cabe aqui citar o estudo de Gans (1966)¹⁶ sobre a subespeciação de *Amphisbaena darwini*, apontando o rio Uruguai entre Rio Grande do Sul e a Argentina como dentro de uma zona de intergradação entre duas subespécies.

O *Centro de Dispersão Uruguaio* situa-se no Uruguai e, como está confinado pelo oceano Atlântico à direita, Río de La Plata ao sul e Uruguai a oeste, sua dispersão é para o norte, atingindo o sul do Rio Grande do Sul. Algumas formas dispersam-se até as bordas do planalto, outras escalam-no, mas nenhuma atinge as partes altas do nordeste; poucas sobem pelo Planalto Médio, como *Lystrophis dorbignyi*.

PROVÍNCIAS LIMÍTROFES

A Província Pampeana, que pertence à sub-região Andino-Patagônica, recebe ofiofauna das Províncias Tupi, Guaraní e Bororó, da sub-região Guiano-Brasileira.

A Província Tupi entra pelo extremo nordeste do Rio Grande do Sul, mas suas formas estão mais ligadas ao bioma das florestas da encosta do planalto do Brasil. Raras formas seguem para o sudeste desse Estado, e apenas pelas manchas de mata ainda existentes.

A Província Guaraní apresenta o maior número de espécies que se dispersam até o nordeste da Pampeana (Lema *et alii*, m.s.³¹). Um número menor de formas chegam até o lado oriental e centro do Rio Grande do Sul e, mesmo, o Uruguai.

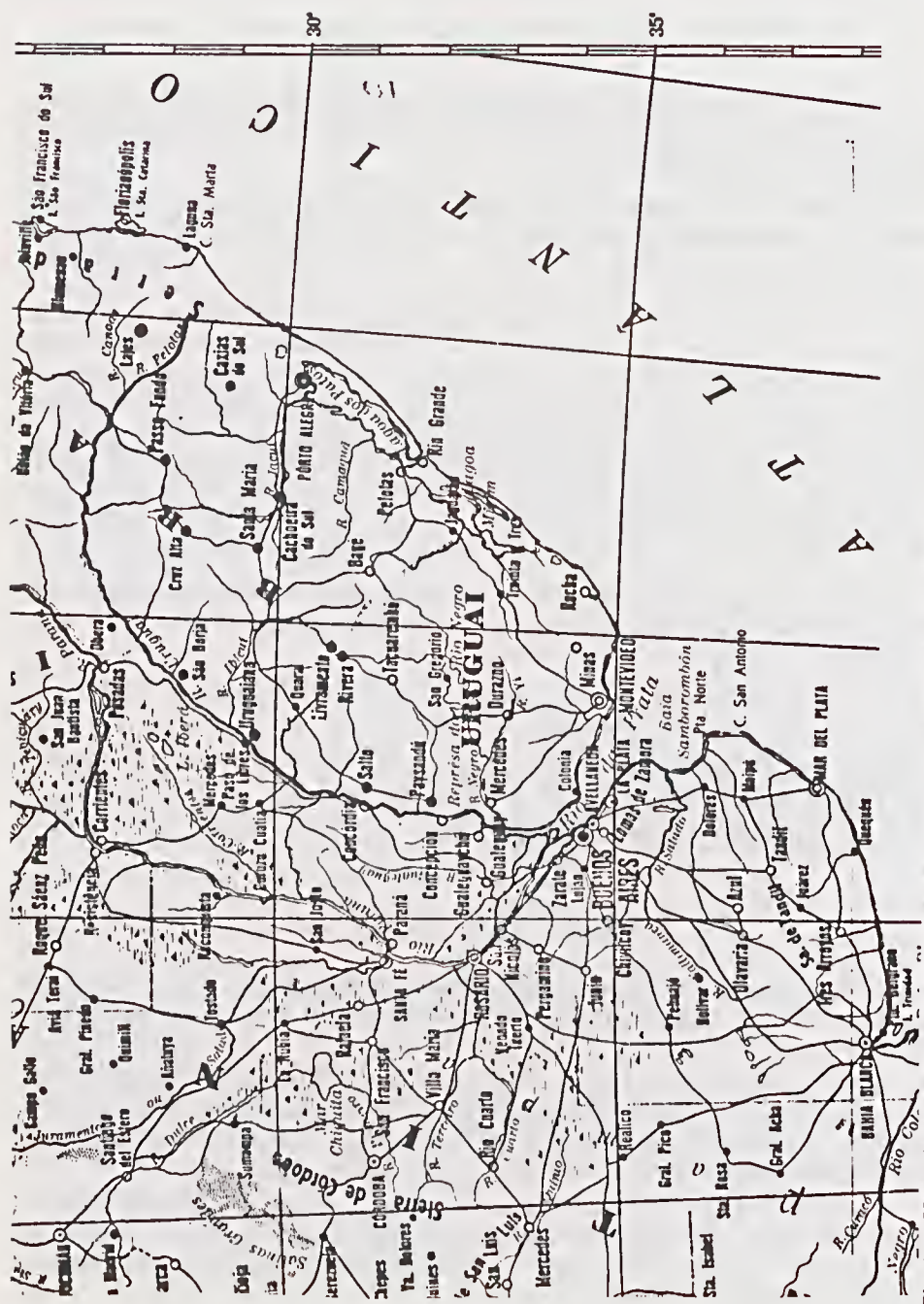


Fig. 1 — Mapa da área física da Provincia Pampeana, com a indicação das altitudes.

A Província Bororo apresenta formas cuja dispersão dá-se para sudoeste atingindo o centro-norte e noroeste do Rio Grande do Sul e a mesopotâmia argentina; um número menor atinge, o noroeste do Uruguai.

Há, ainda, algumas espécies de serpentes que tem distribuição geográfica do tipo continental, desde o norte da América do Sul até o Rio Grande do Sul pampeano e, mesmo, algumas, até o Uruguai.

HISTÓRIA DA DISPERSÃO

Há, pelo menos, três padrões gerais de formas ofídicas na Província Pampeana, que são interpretados aqui, como estágios da especiação.

O primeiro ocupa a região argentina; o segundo, o Uruguai e o sul do Rio Grande do Sul; e o terceiro confina-se à depressão central e encostas do planalto a nordeste no Rio Grande do Sul.

Inicialmente a ofiofauna pampeana era contínua entre o sul do Brasil e a Argentina. O Rio de La Plata era muito estreito, não sendo barreira. Com seu rápido alargamento, bem como dos cursos inferiores do Uruguai e Paraná, houve isolamento daquela biota inicial em duas — uma bona-riente e outra uruguaio-brasileira, que sofreram evolução diferenciada, pelas condições ambientais específicas.

Nos pampas do Uruguai formou-se um grupo de formas próprias. Assim também no lado oriental do Rio Grande do Sul, surgiu um outro grupo de formas próprias, por possuir essa área outras características ambientais.

Como o fluxo genético do Uruguai para o Rio Grande do Sul continua e as subespécies formadas tendem a se encontrar ao longo da região central do Rio Grande do Sul, há, aí uma intensa zona de intergradação, com taxa crescente de genótipos pela segregação de todos os caracteres genotípicos das espécies intergradantes.

Pode ser que, com o passar dos tempos, essa zona de intergradação tenda a criar uma forma nova, enquanto que as formadoras ocupantes das áreas-core atinjam o estágio de isolamento reprodutivo. Os espécimens provenientes da região central do Rio Grande do Sul são de difícil avaliação, se observados isoladamente, pelo menos os pertencentes a espécies com adiantado estado de diferenciação.

Pelo litoral do Uruguai dispersaram-se algumas formas que tomaram rumo norte, povoando a estreita faixa de terra do litoral, que estava confinada entre o oceano e a seqüência de águas contínuas desde o Uruguai até o sul de Santa Catarina. Esse contingente assim isolado e submetido à condições ambientais muito características, modificou-se, criando um padrão de formas próprias daí. Com o levantamento de todo o litoral com o aterro contínuo que continua se operando, esse corpo de água foi se interrompendo oferecendo, atualmente, o aspecto de lagoas de diferentes tamanhos com pontes de terra conectando o litoral com o interior e por onde o contingente litorâneo dispersou-se encontrando-se e integrando com formas pampeanas.

Na espécie *Elapomorphus bilineatus* podemos apreciar uma faixa de intergradação de norte a sul, desde Porto Alegre (Rio Grande do Sul) até Maldonado (Uruguai), da subespécie do litoral, *E. bilineatus trilineatus* com a do pampa, *E. bilineatus lemmiscatus*. A variedade de genótipos aí ocorrentes é enorme e, no passado, alguns deles foram interpretados como espécies diferentes.

Aquelas formas pampeanas que escalaram o planalto meridional do Brasil encontraram-se e intergradaram com as formas do planalto, de dispersão norte-sul. Como o fluxo genético continua nessas áreas, é possível apreciar-se uma forte zona de intergradação de formas do pampa com as do planalto oriental na zona das encostas do mesmo, a nordeste do Rio Grande do Sul.

Outra região em que a mescla de faunas continua se operando é a noroeste do Uruguai e região mesopotâmica, onde há intergradação de formas uruguaias com argentinas e com sul-riograndenses. (Fig. 2)

Apesar de não ter sido examinada a variação geográfica de todas as espécies pampeanas, o exame que estamos procedendo em algumas delas, vem confirmando o exposto.

COMPOSIÇÃO FAUNÍSTICA

As espécies mais características da Província Pampeana são as que seguem, em ordem sistemática:

Família Leptotyphlopidae — *Leptotyphlops munoai*: do Uruguai para o sul do Rio Grande do Sul.

Família Colubridae — Subfamília Colubrinae — *Helicops carinicaudus infrataeniatus*: de São Paulo para o Uruguai e Argentina; também do alto Paraná para o Río de La Plata flutuando em jangadas de *Eichornia* sp. trazidas pelas cheias do Paraná. *Dryadophis bifossatus bifossatus*: do leste do Brasil para o Rio Grande do Sul. *Liophis miliaris*: de norte a sul do Brasil atingindo todo o pampa platino. *Liophis anomalus*: do centro a sul do Brasil para Uruguai e, para oeste, até a pré-cordilheira de Córdoba, Argentina. *Liophis jageri*: toda a área, desde o centro Paranaense — *Leimadophis poecilogyrus pictostriatus*: do leste uruguaio a sudeste do Rio Grande do Sul. *Leimadophis poecilogyrus plattensis*: da Argentina para sudoeste do Rio Grande do Sul. *Leimadophis almadensis*: até o lado oriental baixo do Rio Grande do Sul. *Lygophis flavifrenatus*: litoral norte e centro-oriental do Rio Grande do Sul. *Chironius bicarinatus*: segue de norte a sul pelos capões orientais do pampa do Rio Grande do Sul.

Família Colubridae — Subfamília Heterodontinae — *Lystrophis dorbignyi*: toda a pampeana, com subespécies em estudo — *Lystrophis semicinctus*: da Argentina para o oeste do Rio Grande do Sul e noroeste do Uruguai. *Waglerophis merremii*: do planalto para o nordeste baixo do Rio Grande do Sul.

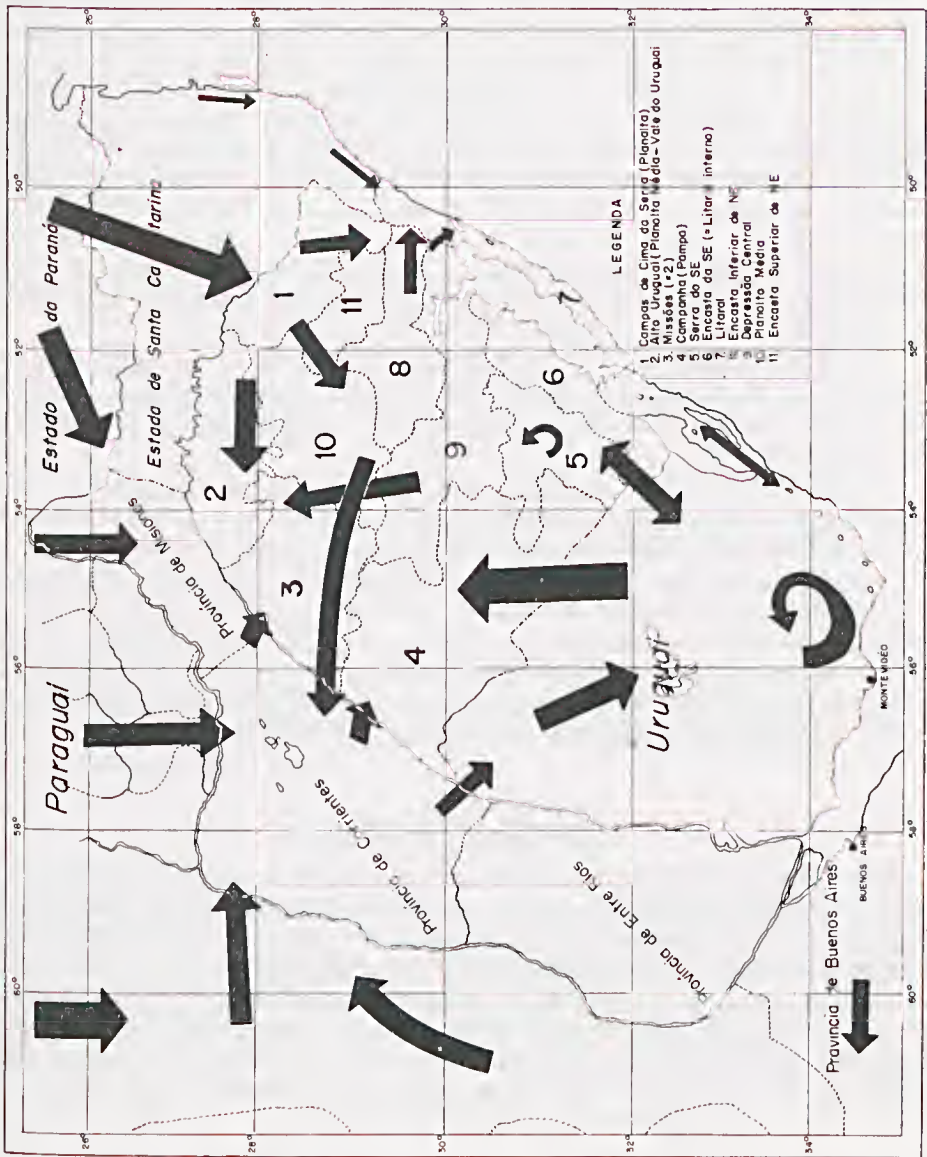


Fig. 2 — Linhas de dispersão na zona abrangente pelo Rio Grande do Sul.



Família Colubridae — Subfamília Boiginae — *Oxyrhopus rhombifer*: toda a Província; apresenta variações que estamos começando a examinar. *Philodryas aestivus subcarinatus*: do Uruguai para o Rio Grande do Sul intergradando com a forma nominal na encosta do planalto no Rio Grande do Sul. *Philodryas patagoniensis*: de norte a sul, a toda a Província Pampeana; com variações. *Philodryas olfersii*: de norte a sul, até os capões dos pampas no Rio Grande do Sul e Argentina; também apresenta variações geográficas. *Clelia rustica*: do leste do Brasil para o Uruguai e Argentina; com variações. *Clelia occipitolutea*: de norte a sul até o norte do Uruguai e Argentina; com subespécies em estudo por J. R. Bailey (Durham, N. Car., E.U.A.). *Tantilla melanocephala*: de norte a sul, até nordeste do Rio Grande do Sul e norte do Uruguai e Argentina. *Tomodon ocellatus*: Argentina ao sul do Rio Grande do Sul e Uruguai. *Tomodon dorsatus*: do centro do Brasil para o nordeste do Rio Grande do Sul. *Elapomorphus tricolor*: do oeste do Brasil para a Argentina e noroeste do Uruguai. *Elapomorphus bilineatus*: toda a Pampeana e Guaraní, com subespécies características dos diferentes centros (LEMA²⁷). *Pseudablabes agassizii*: da Guaraní para o Uruguai, com variações.

Família Colubridae — Subfamília Dipsadinae — *Sibynomorphus turgidus*: da Guaraní para Argentina, noroeste do Uruguai e oeste do Rio Grande do Sul. *Sibynomorphus ventrimaculatus*: da Guaraní para o Rio Grande do Sul.

Família Micruridae — *Micrurus corallinus*: da Guaraní para o Rio Grande do Sul, Argentina e noroeste do Uruguai (só nas partes elevadas). *Micrurus frontalis altirostris*: do Uruguai para o Rio Grande do Sul.

Família Viperidae — Subfamília Crotalinae: *Bothrops alternatus*: da Guaraní para a Argentina, Uruguai e todo o Rio Grande do Sul — *Bothrops neuwiedi pubescens*: do Uruguai para o Rio Grande do Sul subindo as encostas de nordeste do planalto. *Bothrops neuwiedi diporus*: na Argentina. *Crotalus durissus terrificus*: da Guaraní para o Rio Grande do Sul e lado oriental elevado do Uruguai e Argentina.

ÁREAS ESPECIAIS

Há áreas na Província Pampeana que apresentam diferenciações próprias, formando genótipos à parte. As elevações a sudeste do Rio Grande do Sul e ao sul de Buenos Aires, parecem ser zonas de endemismo, como se constatou com *Elapomorphus bilineatus* (LEMA¹⁷).

As elevações do sudeste do Rio Grande do Sul citadas acima (Serra de Sudeste), seguem até o sudeste do Uruguai e a maioria das espécies de répteis aí ocorrentes são melanísticas. Isso é notável em *Lystrophis dorbignyi*, *Elapomorphus bilineatus* e *Micrurus frontalis altirostris*.

COMENTÁRIOS E CONCLUSÕES

As poucas espécies de serpentes próprias dos pampas apresentam variação geográfica que ainda não foi analisada. Assim, as conclusões definitivas sobre essa variação só poderão ser formuladas quando isso for feito.

Essas três áreas de diferenciação geográfica (bonariense, uruguaia e centro-oriental) podem representar áreas de subespécies — ao menos para as espécies distribuídas em toda a Província Pampeana. Isso foi visto em *Elapomorphus bilineatus* (LEMA, 1976²⁷), está sendo visto em *Lystrophis dorbignyi* e outras.

Assim, também, com respeito a espécies do Centro de Dispersão Paranense e que se dispersam para o sul; e formas que se dispersam do Uruguai para as encostas da Serra do Mar, encontram-se as subespécies cruzando-se e produzindo intergradantes.

A região do planalto no Rio Grande do Sul está sendo reexaminada. Mas faltam muitos exemplares, principalmente de Santa Catarina, que possam indicar até que ponto a ofiofauna oriental atinge em sua dispersão para o sul.

SUMMARY: The zoogeographic Pampean Region extends since Southern Brazilian Plateau borders to savannahs of Uruguay and north-eastern Argentina. There are, at least, two Dispersion Centers, the Bonariensis, and the Uruguayan. The most forms of Rio Grande do Sul, Brasil, are from Uruguayan Center. By the North of the Pampean Region arrive subtropical and tropical snake forms, proceeding of the Serra do Mar, Paranensis, and Paraná basin Centers. North of Rio Grande do Sul and Argentina is a transitional area between two bigs zoogeographic divisions: the Guyano-Brazilian, and Andino-Patagonian Subregions.

In Rio Grande do Sul there are many intergradations that result of the meeting of forms of different Zoogeographic Provinces, Tupi, Guarany, Bororo, and Pampean.

It's present an hypothesis on the dispersion history of the Pampean snake-fauna.

KEY WORDS: Províncias Zoogeográficas. América do Sul. Brasil. Argentina. Uruguai. Rio Grande do Sul. Misiones. Corrientes. Entre Rios. Buenos Aires. Centros de Dispersão Bonariense, Uruguai, Serra do Mar e Paranense. Variação Geográfica. Endemismo. Subespeciação. Savana.

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ESTADO ACTUAL DE LA COLECCION HERPETOLOGICA DEL MUSEO DE ZOOLOGIA DE LA UNIVERSIDAD DE CONCEPCION (M.Z.U.C.) EN LA PARTE SERPENTES

Tomas CEKALOVIC K.*

RESUMEN: El presente trabajo comprende la colección herpetológica (parte serpentes) de la Facultad de Ciencias Biológicas y de Recursos Naturales de la Universidad de Concepción, la cual tiene depositados 662 ejemplares correspondientes a 179 especies repartidas en 73 géneros que representan 8 familias.

INTRODUCTION

La colección Herpetológica (parte Serpentes) del Museo de Zoología del Departamento de Zoología, Facultad de Ciencias Biológicas y de Recursos Naturales de la Universidad de Concepción, Chile, se encuentra guardada en muebles metálicos: Reptilia 007 a Reptilia 012, los ejemplares guardados en frascos de diversos tamaños en alcohol 70%, cada especie con su etiqueta numerada está depositada en frascos independientes, al existir varios ejemplares de una determinada especie, estos se guardan en un solo frasco, como cada ejemplar lleva una etiqueta amarrada y numerada, es fácil ubicarlo en el fichero kárdex específico, en el cual, ordenados sistemáticamente, se anotan los datos de: Orden, Familia, Género, especie, país y localidad de procedencia o captura, fecha, colector, N.º de estación en caso de expediciones o viajes, número de ejemplares, determinador y otros datos (si fueren necesarios), en la ficha queda señalado si son ejemplares tipos (Holo, Alo, Para, Lecto, Topo etc.), anotándose la información bibliográfica de la primera descripción.

Los ejemplares tipos se guardan en frascos con tapas rojas, que no se utilizan para otros fines. La información sobre las especies existentes se agregan a un Catálogo de especies que se actualiza cada vez que se incorporan algunos lotes nuevos.

La lista de los tipos se ha publicado por T. Cekalovic y J. N. Artigas en 1981.

El resumen de la colección es el siguiente:

* Museo de Zoología de la Universidad de Concepción — Chile.

SERPENTES

Fam. Boidae — Ejemplares

- Boa* — 2 especies (2) — Venezuela, Argentina
Corallus — 1 especie (2) — Ecuador
Epicrates — 3 especies (7) — Ecuador, Argentina, Venezuela
Erix — 1 especie (1) — Rusia

Fam. Hydrophiidae

- Pelamis* — 1 especie (1) — Chile

Fam. Leptotyphlopidae

- Leptotyphlops* — 3 especies (7) — Venezuela, U.S.A.

Fam. Pythonidae

- Morelia* — 1 especie (1) — Australia

Fam. Colubridae — Ejemplares

- Alsophis* — 1 especie (2) — Chile
Arizona — 1 especie (1) — U.S.A.
Atractus — 5 especies (6) — Ecuador, Paraguay, Bolivia
Boaedon — 1 especie (2) — Africa
Chironius — 5 especies (5) — Bolivia, Brasil, Venezuela
Coluber — 2 especies (2) — U.S.A., Italia
Cyclagras — 1 especie (1) — Bolivia
Dendroaspis — 1 especie (1) — Africa
Diadophis — 1 especie (1) — U.S.A.
Dipsas — 2 especies (4) — Ecuador, Perú, Venezuela
Dromicus — 4 especies (138) — Cuba, Chile, Haití
Drymarchon — 3 especies (3) — Venezuela, U.S.A.
Drymobius — 2 especies (2) — Perú, U.S.A.
Elaphe — 5 especies (5) — Rusia, U.S.A.
Elapomorphus — 1 especie (1) — Uruguay
Erythrolamprus — 1 especie (1) — Venezuela
Helicops — 1 especie (2) — Venezuela
Heterodon — 1 especie (1) — U.S.A.
Imantodes — 1 especie (1) — Venezuela
Incaspis — 1 especie (1) — Perú
Lampropeltis — 1 especie (4) — U.S.A.
Leimadophis — 7 especies (19) — Paraguay, Venezuela, Argentina, Bolivia, Perú
Leptodeira — 3 especies (32) — Ecuador, Argentina, Venezuela
Leptophis — 4 especies (6) — Paraguay, Venezuela
Liophis — 2 especies (6) — Argentina, Brasil
Lycophidion — 1 especie (1) — Africa
Lygophis — 1 especie (3) — Venezuela

- Lystrophis* — 2 especies (6) — Argentina, Paraguay
Masticophis — 3 especies (4) — Venezuela, U.S.A.
Mastigodryas — 7 especies (22) — Venezuela, Paraguay, Brasil
Natrix — 7 especies (11) — U.S.A., Rusia
Nerodia — 2 especies (2) — U.S.A.
Ninia — 1 especie (2) — Venezuela

Fam. Colubridae — Ejemplares

- Opheodrys* — 1 especie (2) — U.S.A.
Oxybelis — 3 especies (8) — Venezuela, Bolivia
Oxyrhopus — 4 especies (9) — Venezuela, Argentina, Bolivia
Paraguay
Philodryas — 5 especies (9) — Argentina, Chile, Bolivia
Philothammus — 2 especies (2) — Uganda
Phimophis — 1 especie (1) — Venezuela
Pituophis — 1 especie (1) — U.S.A.
Psammophis — 1 especie (2) — Africa
Pseudoboa — 2 especies (10) — Ecuador, Venezuela
Pseustes — 1 especie (1) — Venezuela
Regina — 2 especies (2) — U.S.A.
Sibon — 1 especie (5) — Honduras, Venezuela
Sybinomorphus — 1 especie (4) — Argentina
Siphlophis — 1 especie (1) — Bolivia
Sonora — 1 especie (1) — U.S.A.
Spilotes — 2 especies (4) — Venezuela, Paraguay
Storeria — 1 especie (1) — U.S.A.
Synophis — 1 especie (1) — Bolivia
Tachymenis — 3 especies (219) — Chile
Tantilla — 3 especies (3) — Venezuela, U.S.A.
Thamnodynastes — 2 especies (5) — Venezuela, Bolivia
Thamnophis — 6 especies (7) — U.S.A.
Tomodon — 2 especies (3) — Argentina
Virginia — 2 especies (3) — U.S.A.
Xenodon — 2 especies (5) — Argentina, Perú, Ecuador

Fam. Viperidae

- Bitis* — 1 especie (1) — Africa
Bothrops — 13 especies (24) — Brasil, Argentina, Venezuela,
Ecuador
Vipera — 1 especie (1) — Taiwan

Fam. Elapidae

- Micrurus* — 6 especies (10) — Brasil, U.S.A., Perú, Venezuela,
Bolivia, Argentina

Fam. Crotalidae

- Agkistrodon* — 4 especies (5) — U.S.A.

Crotalus — 8 especies (14) — U.S.A., Brasil, Venezuela

Sistrurus — 1 especie (1) — U.S.A.

Trimeresurus — 1 especie (1) — Tailandia

SERPENTES

Familias: 8

Géneros: 73

Especies: 179

Ejemplares: 662

Continentes: 5

Países (total): 18

Viejo Mundo: Australia, Africa, Rusia, Taiwan, Tailandia, Italia, Uganda.

Nuevo Mundo: Argentina, Chile, Uruguay, Paraguay, Bolivia, Perú, Brasil, Ecuador, Venezuela, U.S.A., Honduras, Cuba, Haití.

ABSTRACT: The present herpetological collection (part Serpentes), of the Facultad de Ciencias Biológicas y de Recursos Naturales of University of Concepción, maintained in deposit amount to 662 specimens, pertaining to 179 species, distributed into 73 genera of 8 families.

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ESTADO ACTUAL DE LA COLECCION ARACHNOLOGICA DEL MUSEO DE ZOOLOGIA DE LA UNIVERSIDAD DE CONCEPCION (M.Z.U.C.), PARTE SCORPIONES

Tomás CEKALOVIC K.*

RESUMEN: La colección de escorpiones del Museo de Zoología de la Universidad de Concepción (M.Z.U.C.), posee actualmente 95 especies identificadas que corresponden a 40 Géneros con 393 ejemplares, se incluye material tipo de 14 especies. Existe también otros 1.250 ejemplares identificados solamente a nivel genérico.

De las siete familias de escorpiones conocidas para el mundo, están seis de ellas representadas en la colección del M.Z.U.C.

INTRODUCCION

La colección Arachnológica (parte Scorpiones), del Museo de Zoología del Departamento de Zoología de la Facultad de Ciencias Biológicas y de Recursos Naturales de la Universidad de Concepción (M.Z.U.C.), se encuentra depositada en un mueble metálico y conservada de acuerdo a normas y técnicas museológicas actuales. Existen en la actualidad 95 especies identificadas que comprenden 40 géneros de 6 Familias, con un total de 393 ejemplares, en este total se incluyen los ejemplares de material tipo de 14 especies (Cekalovic y Artigas, 1981), además se guardan aproximadamente 1.250 ejemplares identificados hasta nivel genérico.

Los ejemplares se conservan en alcohol 70°, en tubos o frascos de vidrio de diversos tamaños, con la correspondiente etiqueta en su interior, cada Género o Familia, según sea el caso es guardado en un frasco de boca ancha de medio o un galón. A cada especie se le confecciona una Ficha específica que lleva los siguientes datos: Orden, Familia, Género y especie, anotándose igualmente el país, lugar de captura, fecha y colector, en otra columna se indica el determinador y el número de ejemplares.

* Museo de Zoología de la Universidad de Concepción — Chile.



LISTA DE LAS ESPECIES CONSERVADAS EN EL MUSEO

CLASE: ARACHNIDA

ORDEN: SCORPIONES

FAMILIA: BOTHRIURIDAE Simon, 1880

GÉNERO: *BOTHRIURUS* Peters, 1861

- Bothriurus araguayae* Vellard, 1934 — 4 ejemplares: Brasil
Bothriurus asper araguayae (Vellard), 1934 — 6 ejemplares: Brasil
Bothriurus bonariensis (C. L. Koch), 1842 — 4 ejemplares: Uruguay
Bothriurus bücherli San Martin, 1963 — 2 ejemplares: Uruguay
Bothriurus burmeisteri Kraepelin, 1894 — 1 ejemplar: Argentina
Bothriurus patagonicus Maury, 1968 — 2 ejemplares: Argentina
Bothriurus conspicuos Mello-Leitão, 1934 — 1 ejemplar: Argentina
Bothriurus wilhelmi Cekalovic, 1976 — 3 ejemplares: Chile

GÉNERO: *BRACHISTOSTERNUS* Pocock, 1894

- Brachistosternus artigasi* Cekalovic, 1974 — 2 ejemplares: Chile
Brachistosternus donosoi, Cekalovic, 1974 — 2 ejemplares: Chile
Brachistosternus psamophilus Maury, 1968 — 1 ejemplar: Argentina
Brachistosternus (Brachistosternus) ehrenbergi (Gervais), 1841 — 5 ejemplares: Perú
Brachistosternus (Leptosternus) alienus Lönnberg, 1898 — 1 ejemplar: Argentina
Brachistosternus (Leptosternus) negrei Cekalovic, 1975 — 1 ejemplar: Chile
Brachistosternus pegnai Cekalovic, 1969 — 1 ejemplar: Ecuador
Brachistosternus (Microsternus) ferrugineus (Thorell), 1876 — 1 ejemplar: Perú
Brachistosternus intermedius Lönnberg, 1902 — 1 ejemplar: Argentina
Brachistosternus weijenbergi (Thorell), 1876 — 1 ejemplar: Argentina

GENERO: *CENTROMACHETES* Lönnberg, 1897

- Centromachetes pocoki* (Kraepelin), 1894 — 20 ejemplares: Chile
Centromachetes titschaki (Werner), 1939 — 1 ejemplar: Chile

GENERO: *CERCOPHONIUS* Peters, 1861

- Cercophonius michaelseni* Kraepelin, 1908 — 1 ejemplar: Western Australia
Cercophonius sulcatus Kraepelin, 1908 — 1 ejemplar: Western Australia

GENERO: *OROBOTHRIURUS* Maury, 1975

- Orobothriurus dumayi* (Cekalovic), 1974 — 13 ejemplares: Chile

GERENO: *PHONIOCERCUS* Pocock, 1893

- Phoniocercus pictus* Pocock, 1893 — 7 ejemplares: Chile
Phoniocercus sanmartini Cekalovic, 1968 — 47 ejemplares: Chile

GENERO: *TEHUANKEA* Cekalovic, 1973

Tehuanka moyanoi Cekalovic, 1973 — 9 ejemplares: Chile

GENERO: *TIMOGENES* Simon, 1881

Timogenes (Latigenes) mapuche Maury, 1975 — 1 ejemplar: Argentina

GENERO: *UROPHONIUS* Pocock, 1893

Urophonius corderoi Mello-Leitao, 1931 — 7 ejemplares: Chile

Urophonius granulatus Pocock, 1898 — 7 ejemplares: Chile

Urophonius payneensis San Martin y Cekalovic, 1968 — 11 ejemplares: Chile

Urophonius tregualemuensis Cekalovic, 1981 — 3 ejemplares: Chile

Urophonius tumbesis Cekalovic, 1981 — 6 ejemplares: Chile

FAMILIA: BUTHIDAE Simon, 1879

GENERO: *ANANTERIS* Thorell, 1891

Ananteris cussiini Borelli, 1910 — 2 ejemplares: Venezuela

GENERO: *ANDROCTONUS* Hemprich & Ehrenberg, 1829

Androctonus australis hector C. L. Koch, 1839 — 1 ejemplar: Africa

GENERO: *BUTHACUS* Birula, 1908

Buthacus minox occidentalis Vachon et Stockmann, 1968 — 4 ejemplares: Africa

GENERO: *BUTHUS* Leach, 1815

Buthus occitanus mardochei Simon, 1878, var. *mimeuri* Vachon, 1949 — 1 ejemplar: Africa

Buthus occitanus occitanus (Amoreux), 1789 — 9 ejemplares: España, Africa, Francia

Buthus occitanus paris (C. L. Koch), 1839 — 2 ejemplares: Africa

GENERO: *CENTRUROIDES* Marx, 1899

Centruroides flavopictus (Pocock), 1898 — 1 ejemplar: México

Centruroides gracilis (Latreille), 1778 — 3 ejemplares: México

Centruroides margaritatus (Gervais), 1841 — 1 ejemplar: El Salvador

Centruroides ochraceus (Pocock), 1898 — 1 ejemplar: México

Centruroides sculpturatus Ewing, 1928 — 4 ejemplares: U.S.A.

GENERO: *CENTRURUS* Hemprich et Ehrenberg, 1828

Centrurus clegans Thorell, 1877 — 4 ejemplares: México

Centrurus hoxiui Hoffmann, 1932 — 4 ejemplares: México

Centrurus infamatus infamatus (C. L. Koch), 1845 — 4 ejemplares: México

Centrurus limpidus tecomanus Hoffmann, 1932 — 2 ejemplares: México

Centrurus limpidus limpidus Karsch, 1879 — 5 ejemplares: México

Centrurus suffusus suffusus (Pocock), 1902 — 6 ejemplares: México

GENERO: *ISOMETRUS* Hemprich et Ehrenberg, 1828

Isometrus maculatus (De Geer), 1778 — 40 ejemplares: Chile, Hawai

GENERO: *LEIURUS* Hemprich et Ehrenberg, 1829

Leirus quinquestriatus quinquestriatus Hemprich et Ehrenberg, 1829 —
1 ejemplar: Africa

GENERO: *LYCHAS* C. L. Koch, 1850

Lychas marmoreus marmoreus (C. L. Koch), 1845 — 2 ejemplares:
Western Australis

GENERO: *MICROTITYUS* Kjellesvig-Waering, 1966

Microtityus biordi Gonzáles-Sponga, 1970 — 2 ejemplares: Venezuela

GENERO: *PANDINUS* Thorell, 1876

Pandinus imperator (C. L. Koch), 1842 — 1 ejemplar: Africa

GENERO: *PARABUTHUS* Pocock, 1890

Parabuthus planicauda (Pocock), 1902 — 1 ejemplar: South Africa

GENERO: *RHOPALURUS* Thorell, 1876

Rhopalurus laticauda Thorell, 1876 — 2 ejemplares: Venezuela

GENERO: *TITYUS* C. L. Koch, 1836

Tityus bahiensis (Perty), 1834 — 10 ejemplares: Brasil

Tityus bolivianus argentinus (Borelli), 1899 — 1 ejemplar: Argentina

Tityus clathratus C. L. Koch, 1845 — 2 ejemplares: Venezuela

Tityus discrepans (Karsch), 1879 — 2 ejemplares: Venezuela

Tityus lancini González-Sponga, 1972 — 2 ejemplares: Venezuela

Tityus melanostrichus Pocock, 1893 — 2 ejemplares: Venezuela

Tityus serrulatus Lutz y Mello, 1922 — 13 ejemplares: Brasil

Tityus uruguayensis (Borelli), 1900 — 2 ejemplares: Uruguay

Tityus valerae Scorza, 1954, 2 ejemplares: Venezuela

GENERO: *UROPLECTES* Peters, 1894

Uroplectes lineatus (C. L. Koch), 1845 — 2 ejemplares: South Africa

GENERO: *ZABIUS* Thorell, 1894

Zabius fuscus Thorell, 1894 — 2 ejemplares: Argentina

FAMILIA: CHACTIDAE Laurie, 1896

GENERO: *BROTEOCHACTAS* Pocock, 1893

Broteochactas gollmeri (Karsch), 1879 — 2 ejemplares: Venezuela

GENERO: *CHACTAS* Gervais, 1844

Chactas laevipes (Karsch), 1879 — 2 ejemplares: Venezuela

GENERO: *EUSCORPIUS* Thorell, 1876

Euscorpius carpathicus (Linnaeus), 1767 — 4 ejemplares: Francia

Euscorpius carpathicus sicanus (C. L. Koch), 1839 — 1 ejemplar: Africa

Euscorpius flavocaudalis (De Geer), 1778 — 1 ejemplar: Francia

FAMILIA: DIPLOCENTRIDAE Karsch, 1879

GENERO: *DIPLOCENTRUS* Peters, 1861

Diplocentrus keyserlingi zacatecanus Hoffmann, 19.. — 1 ejemplar: México

FAMILIA: VEJOVIDAE Thorell, 1876

GENERO: *CARABOCTONUS* Pocock, 1893

Caraboctonus keyserlingi Pocock, 1893 — 1 ejemplar: Chile

GENERO: *HADRUROIDES* Pocock, 1893

Hadruroides lunatus (C. L. Koch), 1867 — 4 ejemplares: Perú

GENERO: *HADRURUS* Thorell, 1897

Hadrurus arizonensis (Ewing), 1928 — 5 ejemplares: U.S.A.

Hadrurus hirsutus (Wood), 1863 — 1 ejemplar: U.S.A.

GENERO: *PARUROCTONUS* Werner, 1934

Paruroctonus mesaensis Stahnke, 1957 — 6 ejemplares: U.S.A.

Paruroctonus utahensis (Williams), 1968 — 2 ejemplares: U.S.A.

GENERO: *UROCTONUS* Thorell, 1876

Uroctonus apacheanus Gertsch y Soleglad, 1972 — 3 ejemplares: U.S.A.

GENERO: *VEJOVIS* C. L. Koch, 1836

Vejovis carolinus C. L. Koch, 1843 — 1 ejemplar: U.S.A.

Vejovis coahuilae Williams, 1968 — 3 ejemplares: U.S.A.

Vejovis spinigerus spinigerus Wood, 1863 — 6 ejemplares: U.S.A.

Vejovis vorhiesi Stahnke, 1940 — 4 ejemplares: U.S.A.

FAMILIA: SCORPIONIDAE Pocock, 1893

GENERO: *OPISTHACANTHUS* Peters, 1861

Opisthacanthus africanus Simon, 1876 — 1 ejemplar: Africa

GENERO: *OPISTHOPHTHALMUS* C. L. Koch, 1838

Opisthophthalmus capensis (Herbst), 1800 — 1 ejemplar: South Africa

Opisthophthalmus macer Thorell, 1877 — 1 ejemplar: South Africa

Opisthophthalmus pallidipes C. L. Koch, 1843 — 2 ejemplares: South Africa

GENERO: *PALAMNAEUS* Thorell, 1876

Palamnaeus fulvipes (C. L. Koch), 1838 — 1 ejemplar: Malasia

GENERO: *SCORPIO* Linnaeus, 1758

Scorpio maurus tunetanus Birula, 1910 — 1 ejemplar: Africa

GENERO: *URODACUS* Peters, 1861

Urodacus hoplurus Pocock, 1898 — 1 ejemplar: Western Australia

Urodacus novachollandiae Peters, 1861 — 1 ejemplar: Western Australia

Urodacus planimanus Pocock, 1893 — 1 ejemplar: Western Australia

Urodacus yaschenkoi (Birula), 1903 — 1 ejemplar: Western Australia

Urodacus woodwardsi Pocock, 1893 — 1 ejemplar: Western Australia

SCORPIONES

Familias:	6
Géneros:	40
Especies:	95
Ejemplares:	393
Continentes:	5
Países (total)	16

Número de ejemplares identificados a nivel genérico, aproximadamente 1.250.

Información geográfica:

Viejo Mundo: Australia, Africa, España, Francia, South Africa, Malasia.

Nuevo Mundo: Argentina, Chile, Uruguay, Perú, Brasil, Ecuador, Venezuela, México, El Salvador, Haway, U.S.A.

ABSTRACT: The collection of Scorpions deposited in the Museum of Zoology of the Concepción University (M.Z.U.C.), consists of identified species into 40 genera and 393 specimens including type material of 14 species. There exists also 1.250 specimens determined to the genus level.

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SERPIENTES CROTALINAE DE VENEZUELA

F. SANDNER MONTILLA *

Si todos los ofidiólogos viniéramos a éste, el primer centro herpetológico del mundo, que es Butantan exponiendo determinantes modificaciones a las clasificaciones existentes, se produciría una confusión tan gigantesca, que terminaría con la estabilidad de la sistemática ofídica. Por esta razón debemos seguir la propuesta por el ilustrísimo Dr. Alfonso R. Hoge, quien sin dudas es "El alma de los ofidios de Butantan", pues si la gran estrella que iluminó, después de Vital Brasil, a este Instituto fue la figura insigne de Afranio do Amaral hoy día ya su luz productiva declina, por el "tremendo transcurrir del tiempo", nos ilumina hoy con fuerza, la nueva estrella, que es Hoge, para Butantan y el mundo.

Vengo de la patria de Bolívar a hacer una sugerencia que en nada modifica la magnífica clasificación efectuada por el Dr. Hoge y que es: Si en esta clasificación, de la superfamilia *Viperoidae* aparecen las "Pit Vipers" con tanta importancia, tan numerosa en divisiones y tribus, tan enorme la extensión de su distribución, por Nuevo y Viejo Continente, por qué entonces no volver a reivindicar junto a las dos Familias de *Viperoidae*, también la Familia nuevamente *Crotalidae*, y serían tres las familias de esa Superfamilia, pues *Crotalidae* sustituiría mejor a *Crotalinae* y entonces las Subfamilias de *Crotalidae* serían *Angkistrodontinae* y *Crotalinae*. Así los mismos Géneros partirían de Subfamilias y no de Tribus. De esta manera la primera Subfamilia tendría los Géneros: *Angkistrodon*, *Calloselasma*, *Deinangistrodon*, *Gloydinus* y *Hypnale*. y *Crotalinae*: *Bothrops*, *Lachesis*, *Crotalus*, *Sistrurus*, *Ovophis*, *Trimeresurus* y *Tropidolaemus*.

II

RELATO DE LAS SERPIENTES CROTALINAE DE VENEZUELA:

- | | |
|--------------------------------------------------|------------------------------------------------|
| A — Género <i>Bothrops</i> Wagler | B — Género <i>Crotalus</i> Linneo, 1758 |
| 1 — <i>B. atrox</i> (Linneo, 1758) | 1 — <i>C. pifanorum</i> Sandner Montilla, 1980 |
| 2 — <i>B. bilineatus bilineatus</i> (Wied, 1825) | 2 — <i>C. terrificus cumanensis</i> , 1811 |

* Instituto Venezolano de Ofiología — Caracas-Venezuela.

- 2a— *B. bilineatus smaragdinus* 2a— *C. terrificus ruruima* Hoge, 1966
Hoge, 1966
3 — *B. castelnaudi* Dum. Bibr. 3 — *C. vegrandis* Klauber, 1941
& Dumer., 1854
4 — *B. eneydae* Sandner Montilla, 1976
5 — *B. hyoprora* Amaral, 1935
6 — *B. isabelae* Sandner Montilla, 1979
7 — *B. lanceolatus nacaritae* Sandner Montilla, 1981
8 — *B. lansbergii janisrozei* Peters, 1968
9 — *B. medusa* (Sternfeld, 1920)
10 — *B. brasili* Hoge (antes *B. neglecta*)
11 — *B. schlegelii* (Berthold, 1846)
12 — *B. venezuelae* Sandner Montilla, 1960

C Género *Lachesis* Daudin

- 1 — *Lachesis muta muta* (Linneo, 1766)

III

EL CASO DE CROTALUS DURISSUS:

Desde 1936 y más en 1956, publica L. Klauber en su famoso "Rattlesnakes" que la nominación de *C. terrificus* de Laurenti la sustituye por *C. durissus*: A esta insólita y no razonada decisión debemos oponernos, como se opuso Amaral en su época, debido a que estaría en grave peligro la estabilidad de los nombres y hasta mucha útil labor científica, ya que no pueden caprichosamente y sin razonamientos científicos sustituirse nombres, lo que va además en contra del Código Int. de Nomencl. Zool: Nos oponemos por las tres razones siguientes y que iremos llevar a la Comisión Int. de Nom. Zool:

1) Por lo que en su época advirtió y rechazó Amaral (1944 P. Avulsos Vol. V. N.º 5 Pg. 30) sobre la confusión que produce un cambio así, hecho sin base científica, pues desde 1758 desde que Linneo la describe, hasta 1936 (excepto Cope, pero rectifica luego) no se había referido *Crotalus durissus* para Suramérica por ningún autor científico. Sería entonces un *Nomen oblitum* por Analogía.

2) La descripción que Linneo hizo en 1758 de *C. durissus* no corresponde ni encaja, ni puede corresponder a nuestra cascabel tropical, o sea que Linneo cuando describe el holotipo que se perdió después, no tuvo bajo sus ojos la cascabel tropical, describe así ALBO FLAVOQUE VARIUS MACULIS RHOMBEIS NIGRIS DISCO ALBIS HABITAT AMERICA. Tiene color básico, blanco amarillo con grandes rombos negros, igualito como la *C. horridus* no melánica. y no existe cascabel tropical con rombos negros, nunca nadie la ha visto, por lo tanto no corresponde a la misma cascabel de América tropical la de Linneo sino la siguiente descrita la de Laurenti.

3) Klauber al reconocer subespecíficamente "*terrificus*" para el S. de Suramérica y habiendose demostrado por el No 2 que lo que describió Lin. no puede ser la cascabel tropical, debe considerarse sólo *C. terrificus* como válida y utilizable.

POST-STRIKE TRAILING BEHAVIOR IN RATTLESNAKES

D. CHISZAR *
H. M. SMITH *
A. R. HOGE **

INTRODUCTION:

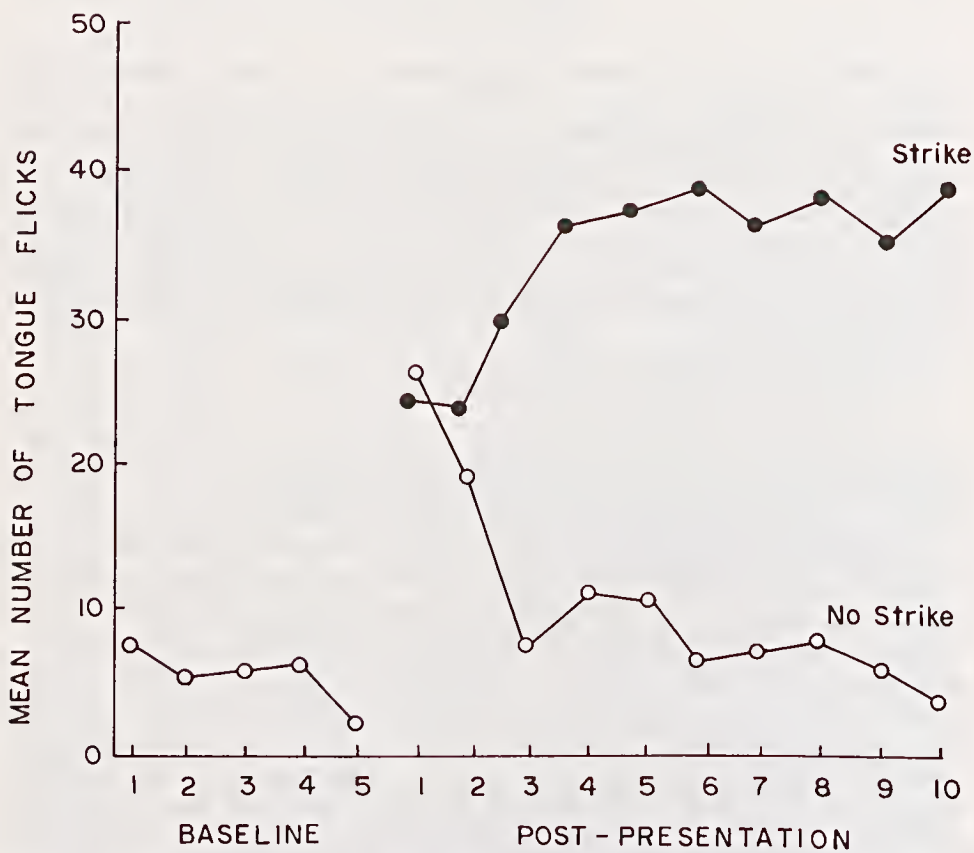
Numerous papers indicate that vipers can follow chemical trails left by rodent prey. Several of these papers also indicate that the snakes are better at following such trails if they have struck and envenomated a rodent just prior to being exposed to chemical trails. Experiments conducted at University of Colorado leave no doubt that the act of striking (and envenomating) a mouse is responsible for the subsequent emission of a sustained, high rate of tongue flicking. Called strike-induced chemosensory searching (SICS), this phenomenon clearly facilitates location and following of chemical trails left by rodents.

REVIEW OF EXPERIMENTS CONDUCTED PRIOR TO 1980

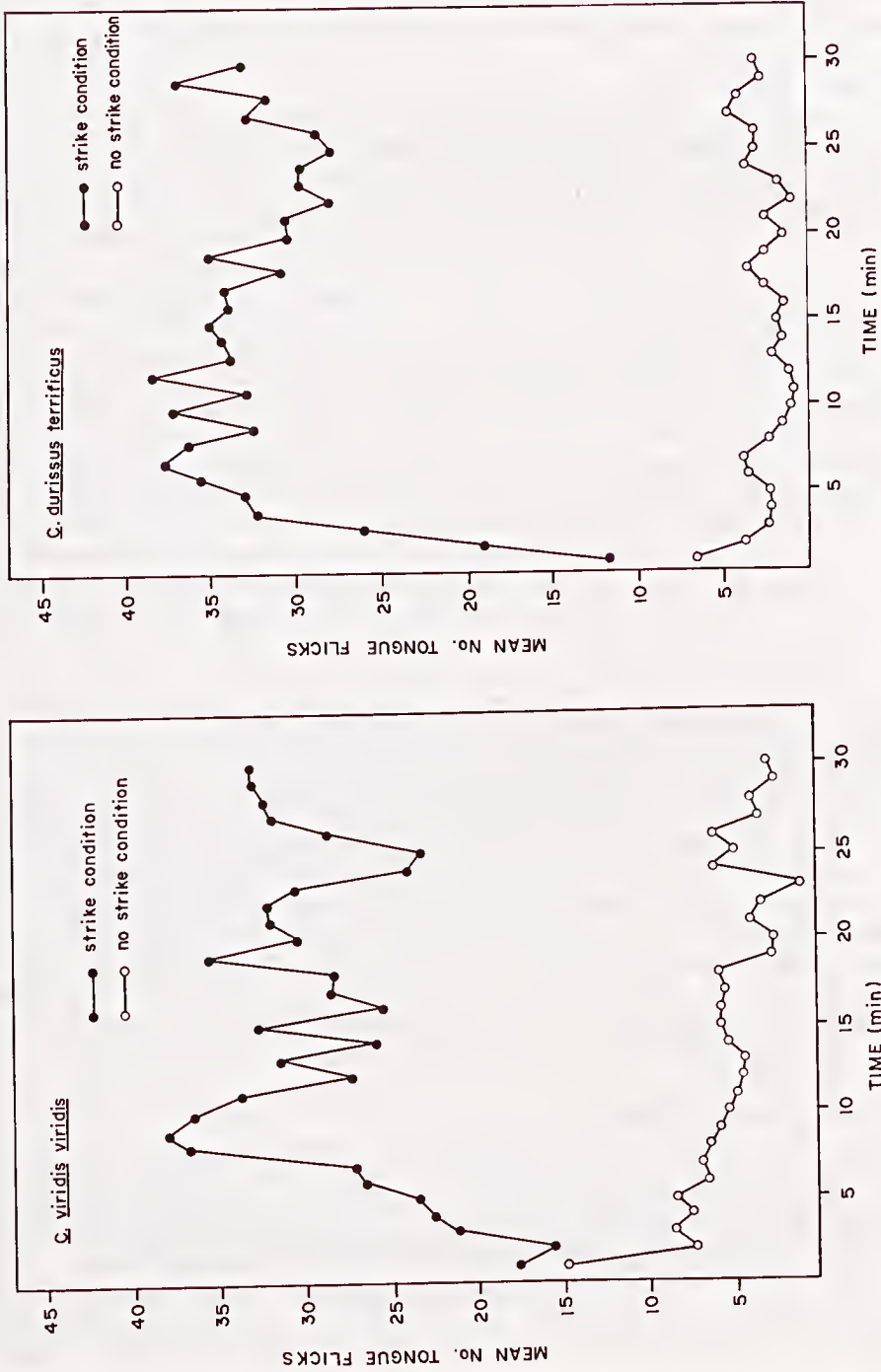
In 1928, F. Baumann found that *Vipera aspis* could distinguish between trails left by nonenvenomated and envenomated mice. Further, the latter type of trail was preferred by *V. aspis*.

Several points should be made before presenting new data. First, SICS is not a consequence of seeing, smelling, or detecting thermal cues arising from mice. An elevation in rate of tongue flicking (RTF) is usually produced by such stimuli, but this elevation is usually small compared to that seen after a rattlesnake delivers a predatory strike. The first slide makes this clear. Initially, rattlesnakes were observed while they were undisturbed in their home cages. RTF was quite low. Then, the snakes were exposed for 3 sec to a live mouse (*Mus musculus*) suspended into the cage but held out of striking range. In one condition the mouse was simply removed and tongue flicks were counted for the next 10 min. In the other condition, the mouse was lowered into striking range, and it was removed immediately after being struck. Again tongue flicks were counted for 10 min. Clearly, RTF increased only in the Strike condition. This is what we mean by SICS. Slide 2 presents a replication of this experiment.

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Slide 1. A typical SICS experiment. A high rate of tongue flicking is seen only after rattlesnakes struck mice, not after seeing, smelling, or detecting thermal cues from mice confined to the odoriferous trail (bottom panel).



Slide 2. This is another SICS experiment. Two taxa are shown and results are quite similar. Note also that SICS continued at asymptotic level for 30 min post-strike.



Another important point is that SICS will continue for as long as 2-3 hours. Even when no chemical trail is present in the snake's post-strike environment, the snake will search for a very long while. Hence, searching behavior is released by the predatory strike, and the high RTF is not dependent upon the presence of chemical stimuli. This is why we have called SICS a fixed action pattern, following Konrad Lorenz's terminology (or a modal action pattern, following George Barlow's terminology).

A third important point is that SICS is a very general phenomenon among rodent-feeding vipers and pit vipers. Most species strike (envenomate) and then release adult rodents, allowing such prey to wander up to 600 cm from the site of attack before succumbing to the venom. Undoubtedly adult rodents are released because they will survive and struggle for a brief period after envenomation (an average of 54 sec for mice envenomated by *C. viridis*). If snakes attempt to hold prey in their mouths during this period, the snakes risk tissue damage from rodent teeth and claws. *B. insularis* strikes and the bird falls mostly damaging the teeth. Hence, natural selection has favored the strategy of releasing rodents after the strike, especially adult rodents. But, this leaves the snake with the task of finding the now-dead rodent (which, incidentally, is no longer emitting movements or thermal cues to attract the snake). Rattlesnakes of all species tested as well as specimens of *Agkistrodon*, *Bitis*, *Bothrops*, *Eristocophis*, and *Vipera* exhibit SICS and trail following. These same snakes show little interest in chemical trails prior to striking, but they have a profound interest in such trails after striking (usually with 2-4 min after the strike). Thus, we conclude that SICS is a widespread solution to the problem of locating envenomated rodent prey.

The fourth point is that once a rattlesnake has begun SICS, it usually will not strike again until the dead mouse has been located and ingested. Although the strike is released by visual and thermal cues arising from rodent prey, the strike in turn releases SICS. It is as if the snake switches its attention from visual and thermal cues to chemical cues. Once the switch has been accomplished, SICS must run to completion before the program can be re-initiated. Usually a single predatory strike is sufficient to cause this perceptual switch. Sometimes, however, several strikes seem to be required. This may be true when the snake has a reduced venom supply so that multiple strikes may be necessary to accumulate an effective dose. Yet, when such a dose has been accumulated through two or three strikes, the snake then switches its attention to chemical cues.

SICS and Trailing Behavior

We have already said that SICS is released by striking — the high RTF is not dependent upon chemical cues in the post-strike environment. But, suppose a rodent trail is available to the snake after a predatory strike has been delivered. How does the snake deal with it?

The answer is that RTF remains relatively constant, whereas the tongue flicks are *directed* to the trail. Hence, the chemical trail does not release the high RTF; it simply exerts a taxic effect on the tongue



flicks. The snake then positions its head so as to keep the flicking tongue in contact with the trail. The result is that the snake's body is gradually drawn along the length of the trail.

An experiment with *Crotalus viridis* makes this clear. Six adult snakes were observed in each of four conditions shown in Slide 3. In two conditions snakes saw but did not strike mice, whereas the snakes struck mice in the remaining two conditions. Then snakes were exposed to a line drawn on the floor of a large cage; the line either contained a rodent chemical trail or it did not contain such a trail. These conditions conform to a 2x2 orthogonal combination of strike vs no strike with presence vs absence of a chemical trail. We recorded: (1) the number of tongue flicks emitted during a 20 min period following the initial mouse presentation, and (2) the number of tongue flicks that were emitted within 2 cm of the solid line.

Slide 4 shows the results of this investigation. Note that snakes emitted high RTFs only after striking mice. Note also that snakes confined tongue flicks to the line only when a strike had been delivered and when the line contained a rodent trail. Hence, rattlesnakes attend to trails, but only after they have struck prey. This conclusion is also supported by calculating the percentage of time snakes spent in contact with the unbroken line in the test apparatus. Slide 5 shows that snakes spent considerable time in contact with this line only when the line contained mouse odor AND only when the snakes had just previously struck a mouse.

This experiment has been replicated twice with results very similar to those reported here.

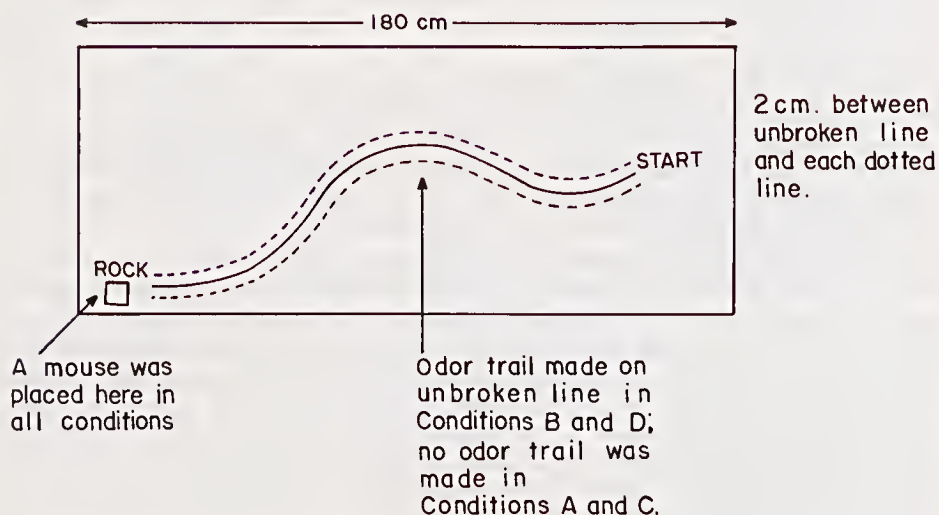
Trails Made by Envenomated Mice and Nonenvenomated Mice

Now that we have developed a methodology for studying chemical trailing behavior in rattlesnakes, we decided to see if rattlesnakes respond differentially to trails made by envenomated and nonenvenomated mice. To accomplish this, we used a situation like that in Slide 6. Snakes were exposed to two trails after striking or after seeing mice. Dependent variables in this study were similar to those described above.

Results are shown in Slide 7. When snakes did not strike mice, they followed neither trail. However, after striking mice, the snakes attended to trails AND they selected the trail made by an envenomated mouse.

The upper panel of slide 7 shows mean percentage of time that snakes spent on either trail. For each snake, time on the envenomated trail was added to time on the nonenvenomated trail; and, this total was divided by the time the snake spent in the apparatus before finding a mouse (a maximum of 20 min was allowed for finding mice). Since the trails occupied about 17% of the floor space of the test apparatus, a snake that moves randomly across the floor should make contact with the trails only about 17% of the time. This is essentially what happened when snakes had not struck mice prior to being exposed to the trail. These animals paid no attention to trails; if they moved at all, they did so in a random fashion. However, when snakes struck mice, SICS was activated and the snakes clearly investigated the trails.

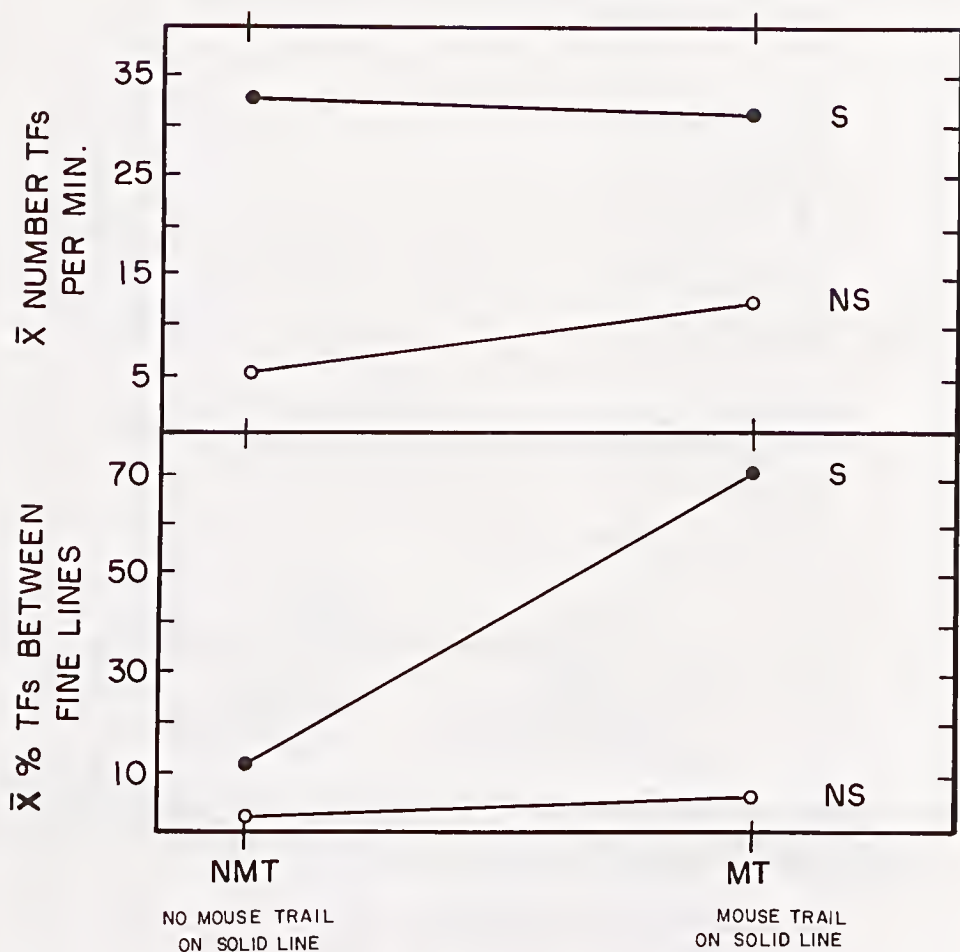
APPARATUS



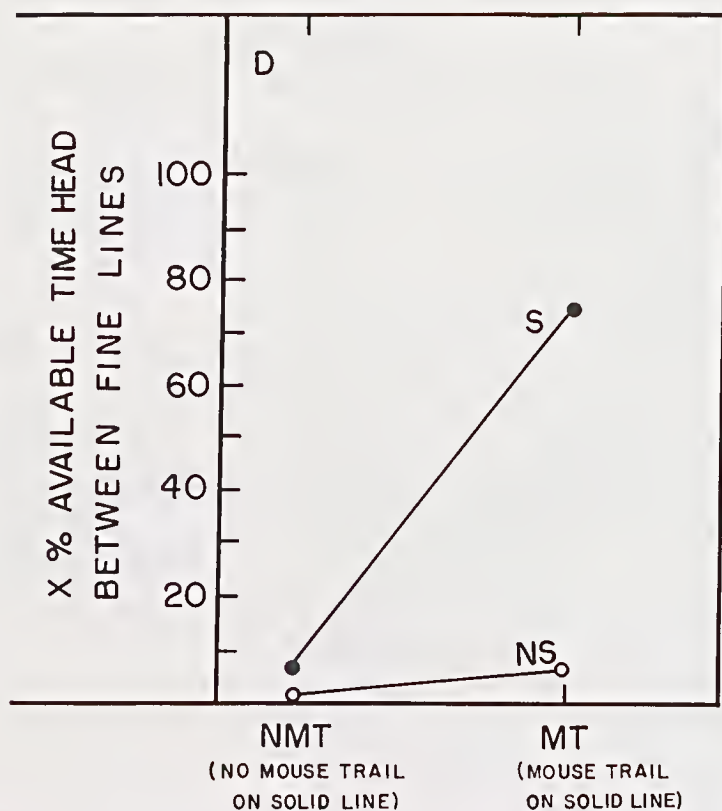
EXPERIMENTAL DESIGN

		MOUSE ODOR TRAIL PRESENT	
		NO	YES
MOUSE PRESENTATION	NO STRIKE	A	B
	STRIKE	C	D

Slide 3. Experimental design and apparatus for the post-strike trailing experiment.

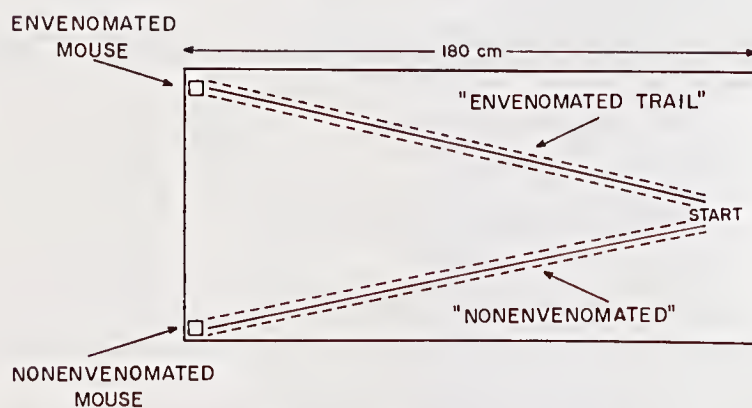


Slide 4. Results of the post-strike trailing experiment. SICS can again be seen (top panel); if snakes struck mice, RTF was high, otherwise RTF was low. Note that tongue flicks were confined to the odoriferous trail (bottom panel).

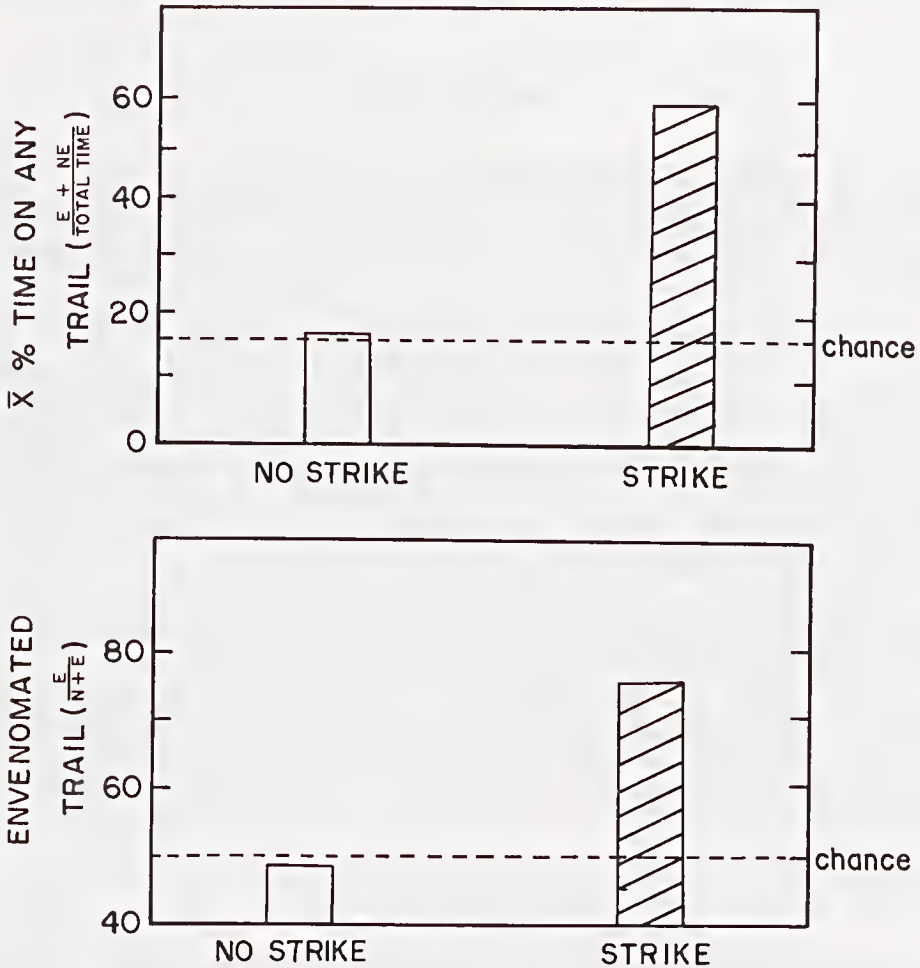


Slide 5. Whereas Slide 4 showed % of tongue flicks confined to the trail, Slide 5 shows the % of time the snakes' heads were confined to the unbroken line. Note that snakes' heads were confined to this line only when they struck mice and when the line contained an odoriferous trail. Hence, this slide agrees with the previous one.

APPARATUS



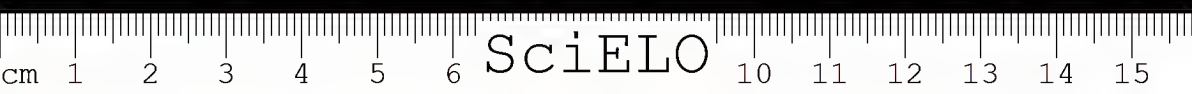
Slide 6. Apparatus for the trail-discrimination experiment. Snakes are exposed to two trails of the same age; one trail was made with an envenomated mouse, the other with a non-envenomated mouse.



Slide 7. Results of the trail-discrimination experiment. Top panel: When snakes had not struck mice prior to being exposed to trails, the snakes did not spend much time investigating the trails. Times spent examining the two trails were summed, and this total was divided by the amount of time the snake was in the apparatus. However, if snakes struck mice prior to being exposed to trails, then the snakes showed considerable interest in the trails. Bottom panel: Here, time on the "envenomated trail" was divided by time spent on both trails. Only snakes which struck mice showed a preference for the trail left by an envenomated mouse.

The lower panel considers only time spent on trails. Time on the envenomated trail was divided by time spent on both trails. If snakes had not struck mice prior to exposure to trails, both trails were contacted equally often. The important data comes from the snakes that struck mice. These snakes clearly preferred the trail made with an envenomated mouse.

We observed 13 snakes in the strike condition. All of them discovered a mouse within 20 min after striking, and 10 snakes (77%)



discovered the envenomated mouse. Six snakes were observed in the no-strike condition; two of them (33%) discovered the envenomated mouse, and four discovered neither mouse within 20 min.

CONCLUSIONS

Strike-induced chemosensory searching has been observed many times in our laboratory as well as in other laboratories. Hence, this is a very reliable phenomenon. The relationship between SICS and trailing behavior is also quite reliable. Hence, it seems reasonable to conceptualize these events as part of the same adaptive suite.

The fact that rattlesnakes preferentially followed trails left by envenomated mice has very important theoretical implications. It is well known that snake venom is very complicated material and that many components of snake venom "are not particularly useful as incapacitating or poisoning agents" (Gans, 1978, p. 7). The present results suggest that some components of venom have evolved not necessarily to subdue prey but rather to enhance the perceptibility of the trail left by envenomated prey. Venom may therefore have not only toxic and digestive significance but also perceptual significance.

Because of these very interesting implications, we feel it is absolutely necessary to replicate the present results before making strong assertions about the perceptual significance of venom.

Accordingly, we conclude that: (1) rattlesnakes are excellent at trailing rodent prey, (2) trailing is seen most clearly after snakes have struck rodent prey, and (3) a trail left by an envenomated rodent *may* be more attractive to a rattlesnake than a trail left by a nonenvenomated rodent.

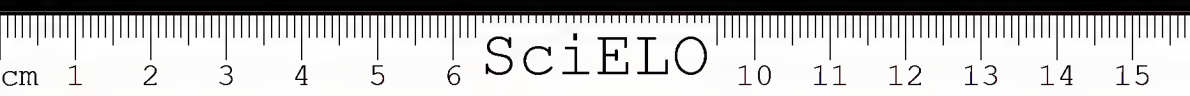
ACKNOWLEDGEMENT

Many persons participated in the experiment here reported: C. W. Radcliffe, T. Miller, K. Stimac, T. Poole, L. Golan, B. O'Connell, K. Scudder, and D. Duvall.

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LEVANTAMENTO DOS GÊNEROS DE OFÍDIOS E ESPÉCIES DE ARACNÍDEOS CAUSADORES DE ACIDENTES NA CASUÍSTICA DO CENTRO DE INFORMAÇÃO TOXICOLÓGICA DO RIO GRANDE DO SUL

(Período compreendido entre 1977 a agosto de 1981)

João Batista TORRES *
Paulo Roque CARLOTTO *

O número de informações que abrangem a área de animais peçonhentos tem crescido aproximadamente de 100% ao ano na casuística do Centro de Informação Toxicológica. Este fato, certamente, está ligado ao maior conhecimento e à maior utilização do serviço de informação por parte das equipes de saúde e pelo público em geral. O aumento da demanda em relação a este tipo de ocorrência nos levou à efetivação de um estudo estatístico a partir do arquivo do CIT-RS.

Para melhor abordagem do tema, analisamo-lo fundamentalmente sob três aspectos:

1. Levantamento dos Gêneros de Ofídios e Espécies de Artrópodos Peçonhentos responsáveis por acidentes na casuística do Centro de Informação Toxicológica do Rio Grande do Sul.
2. Caracterização das pessoas acidentadas por Ofídios e Artrópodos Peçonhentos: faixa etária, região anatômica etc.
3. Finalmente, características que envolvem o Serviço de Informação Toxicológica em relação aos acidentes: intervalo acidente-informação; diagnóstico etiológico (identificação do gênero de ofídio ou espécie de artrópodo peçonhentos causador do acidente).

Síntese de algumas conclusões provenientes destas verificações:

Os acidentes por animais peçonhentos parecem estar ligados a dois fatores importantes — condições climáticas e exposição da população aos agentes;

As aranhas são responsáveis pela maioria das informações e são as maiores causadoras de acidentes, seguidas dos ofídios e, por último, os escorpiões;

* Centro de Informação Toxicológica-SSMA/RS — Brasil.



A faixa etária mais atingida em humanos é de 1 a 14 anos.

Os homens são mais atingidos do que as mulheres nos acidentes ofídicos e escorpiônicos;

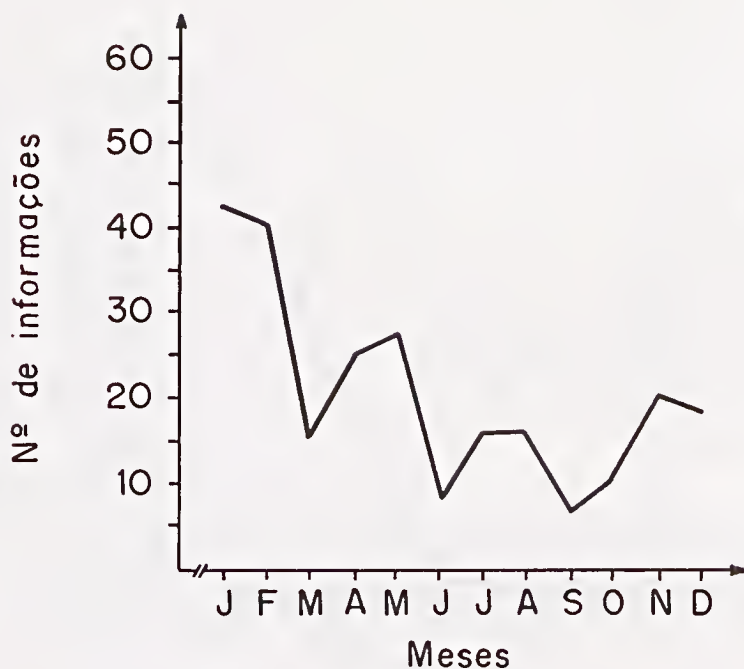
A região anatômica mais atingida nos acidentes ofídicos em humanos é o membro inferior e em maior percentagem pé. Já nos acidentes por aranhas as áreas mais atingidas são os membros superiores;

Sob o ponto de vista de eficácia do Serviço de Informação Toxicológica, o intervalo que vai do acidente até a informação é sempre menor que 24 horas. Os acidentes provocados por *Phoneutria* são os chamados com intervalo mais curto entre acidente e busca de informação. Apenas os acidentes por *Loxosceles* sp. são mais tardios, em geral após 24 horas.

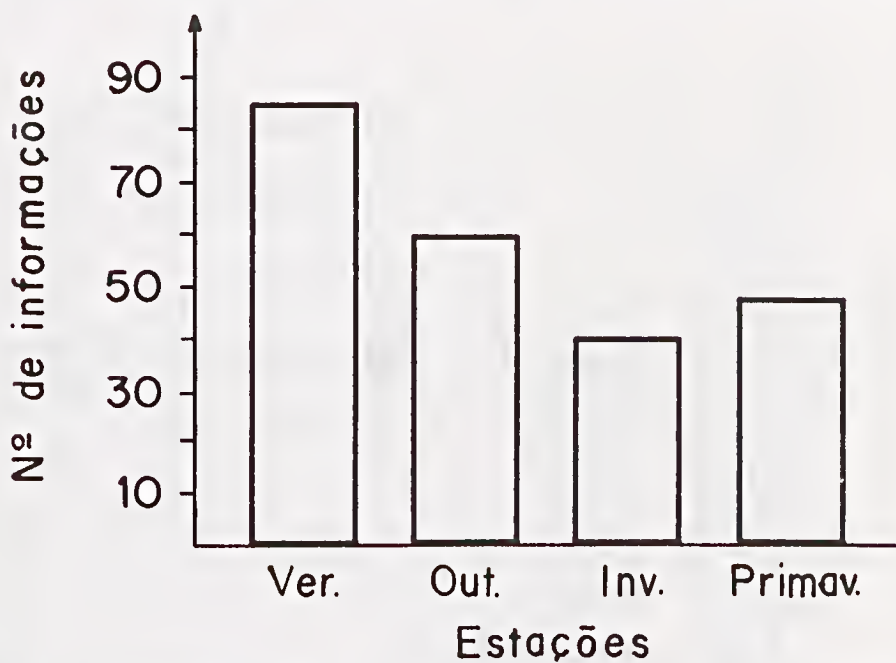
TABELA 1

Tabulação geral e percentagem dos acidentes tóxicos por animais peçonhentos e não peçonhentos na casuística do CIT-RS no período de dezembro de 1977 a agosto de 1981:

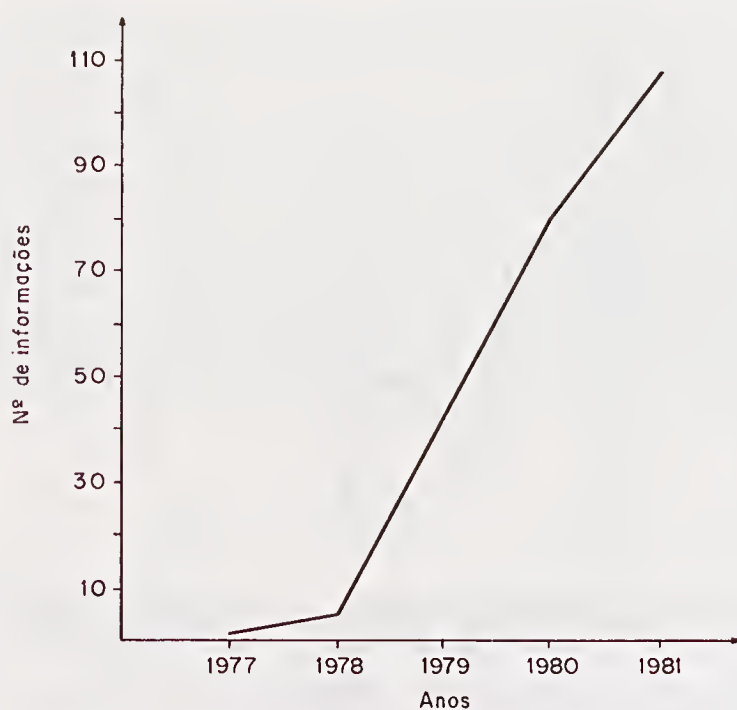
	N.º Acidentes	Percentagem
Aranhas	94	41,59
Ofídios	62	27,43
Escorpiões	29	12,83
Abelhas	8	3,53
Centopéias	6	2,65
Lagartas Urticantes	5	2,21
Formigas	4	1,76
Louva-a-Deus	4	1,76
Vespas	2	0,88
Marimbondos	1	0,44
Lacraias	1	0,44
Peixes Venenosos	1	0,44
Não Identificados	9	3,98
TOTAL	226	100,00



Gráf. 1: Distribuição mensal de informações. Ac. Por animais peçonhentos. (CIT)



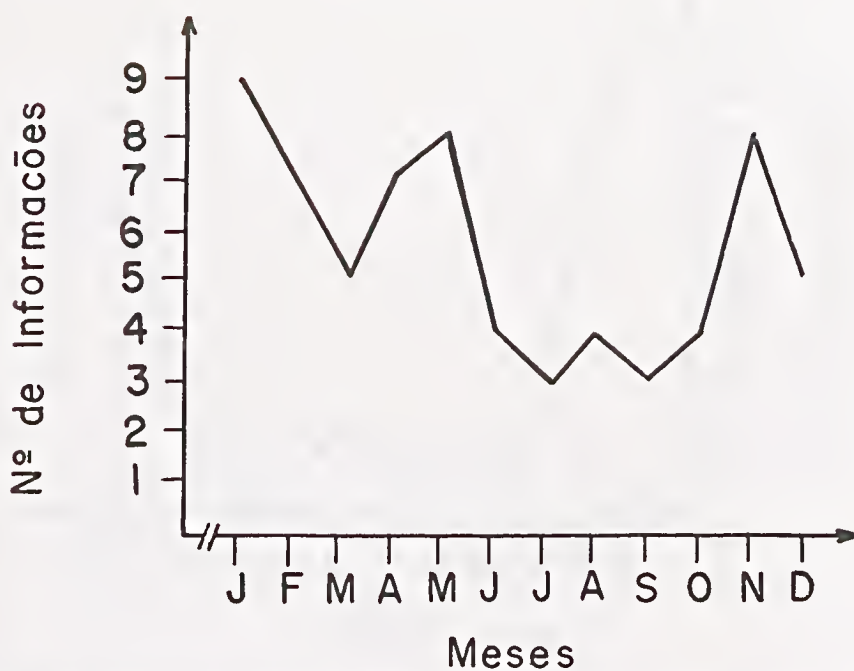
Gráf. 2: Distribuição sazonal. Ac. por animais peçonhentos. (CIT)



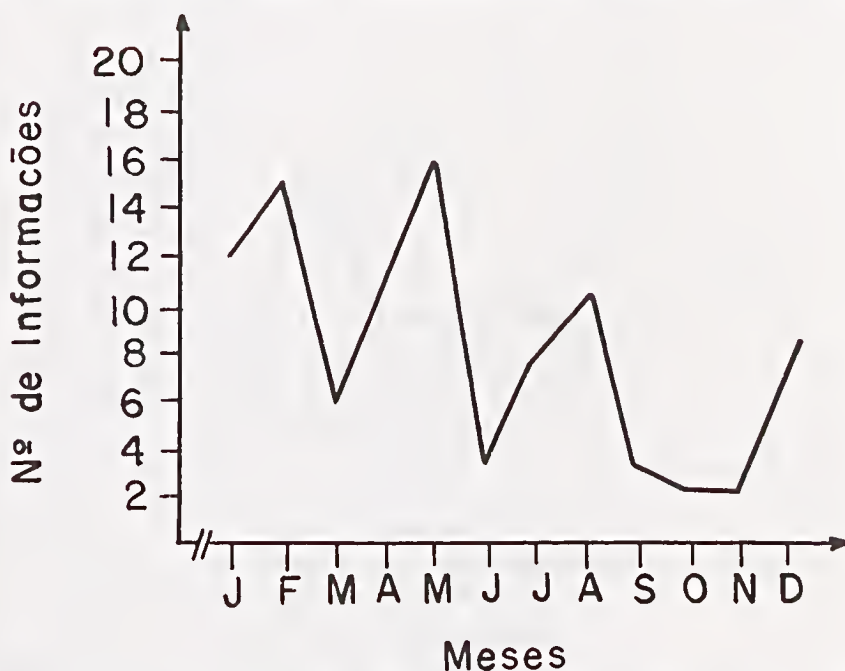
Gráf. 3 : Crescimento do volume de informações sobre acidentes por animais peçonhentos (Centro de Informação Toxicológica)



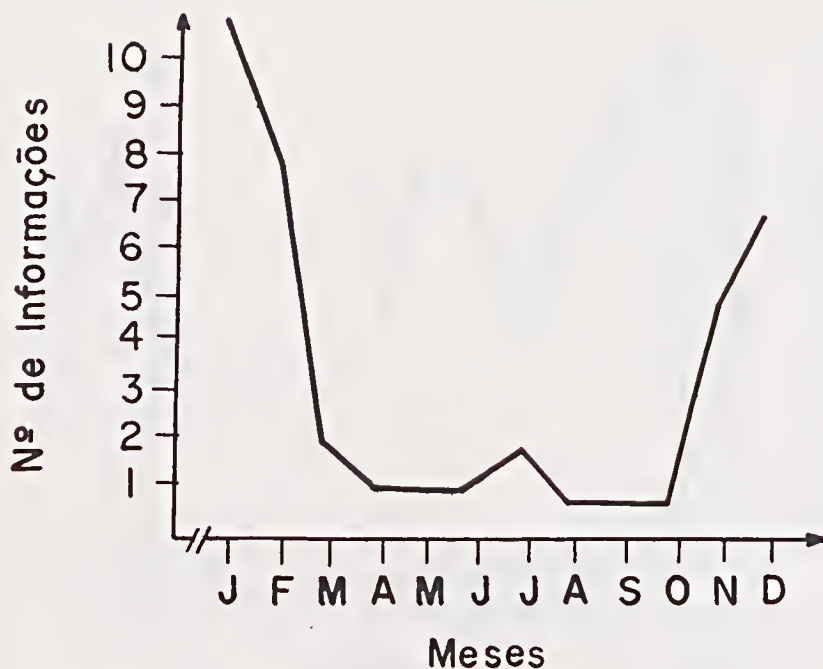
Gráf. 4: Representação dos Acidentes por Aranhas seg. espécie causadora. (CIT)



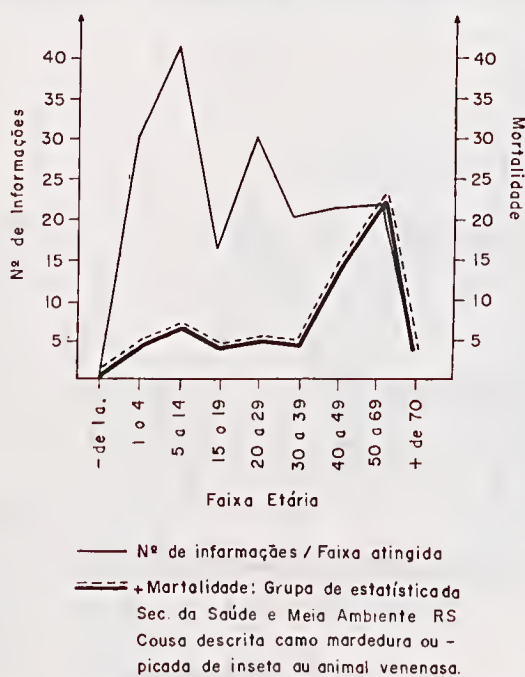
Gráf. 5: Representação mensal de informações sobre acidentes Ofídicos. (CIT)



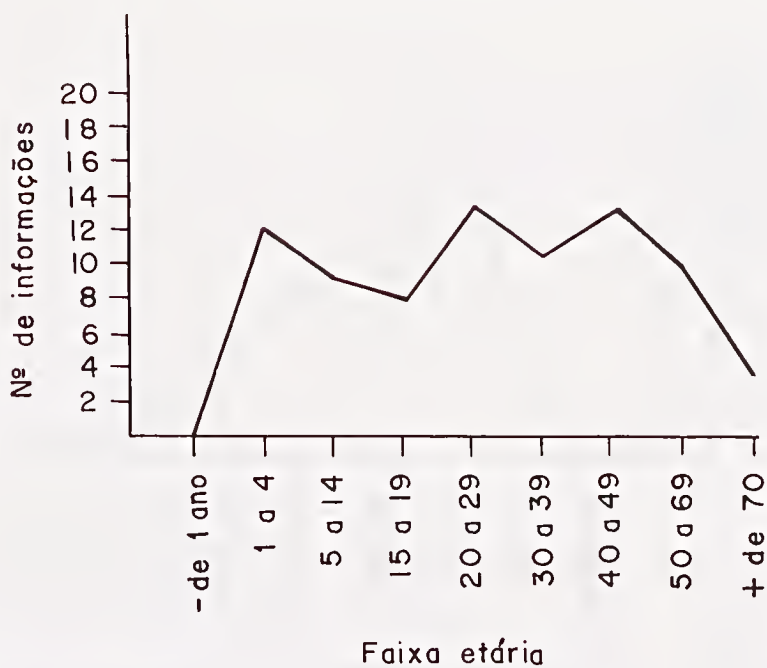
Gráf. 6: Representação mensal de informações sobre acidentes por Aranhas. (CIT)



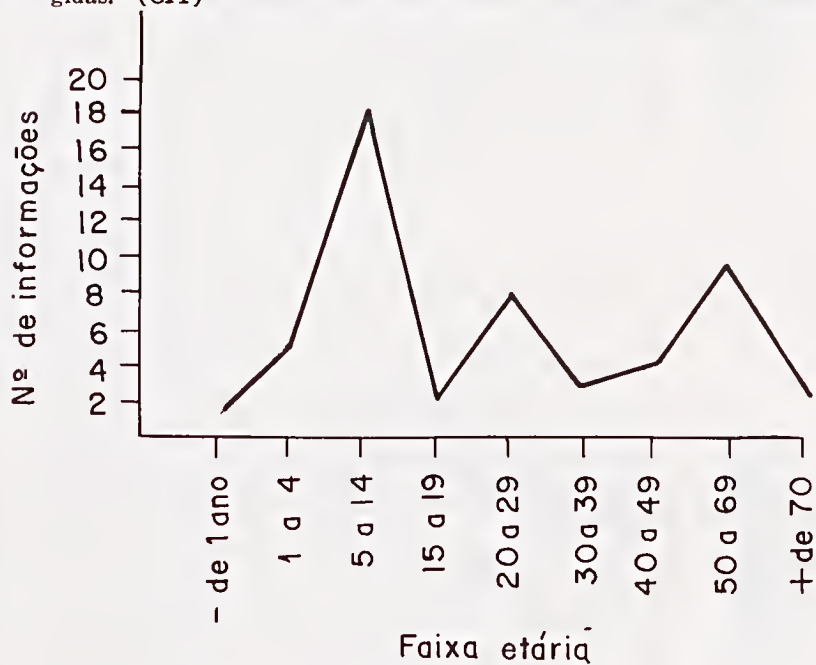
Gráf. 7: Representação mensal de informações sobre acidentes por Escorpiões. (CIT)



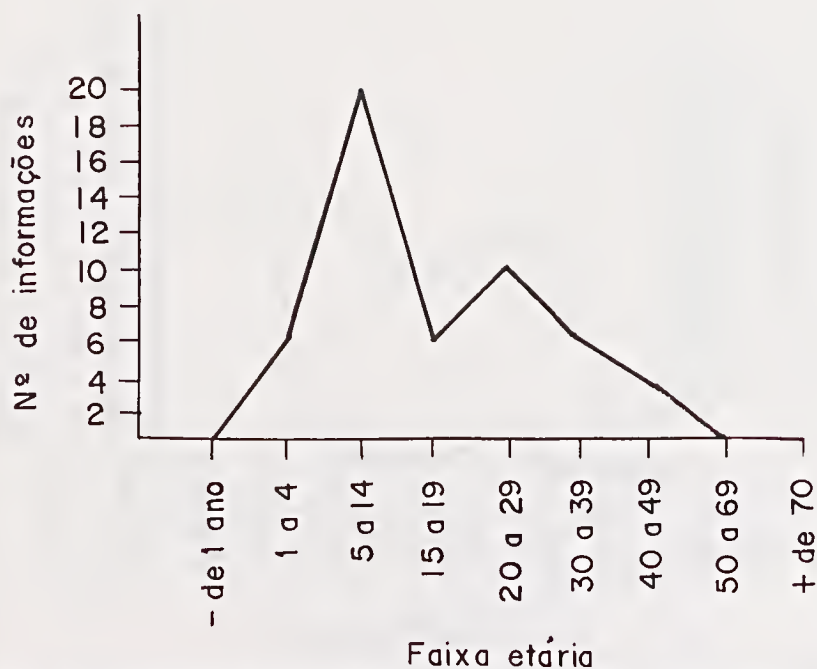
Gráf. 8: Gráfico comparativo N.º de Informações/Mortalidade. (CIT — Grupo de Estatística de Sec. Saúde e Meio Amb. RS)



Gráf. 9: Distribuição de informações sobre Ac. por aranhas. Faixas etárias atingidas. (CIT)



Gráf. 10: Distribuição de informações sobre acid. por Ofídios. Faixas etárias atingidas. (CIT)



Gráf. 11: Distribuição de informações sobre acid. por Escorpíões — Faixas etárias atingidas. (CIT)

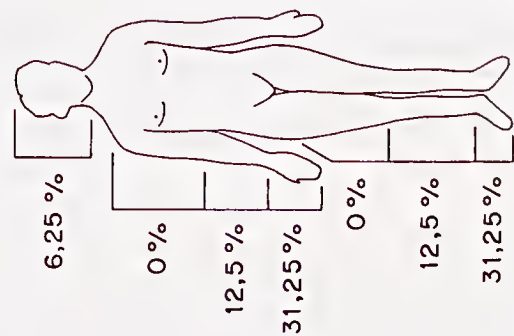


Fig. 1 - Regiões anatômicas atingidas nos acidentes Aracnídeos.

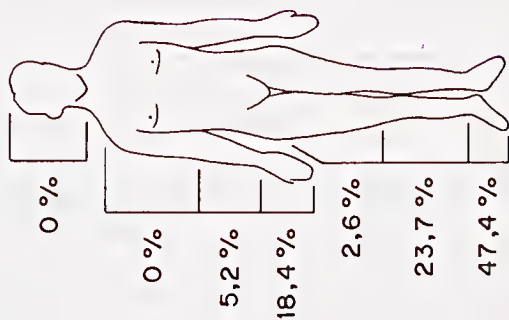


Fig. 2 - Regiões anatômicas atingidas nos acidentes Ofídicos.

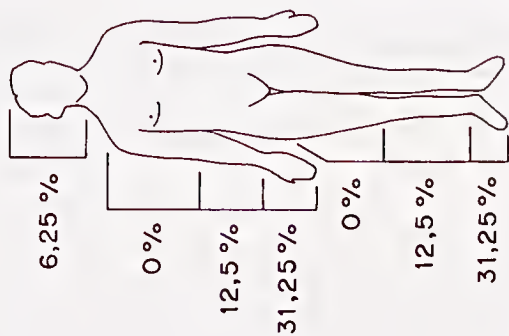


Fig. 3 - Regiões anatômicas atingidas nos acidentes Escorpiônicas.

Fig. 1, 2 e 3 — Representação esquemática das regiões anatômicas mais frequentemente atingidas por animais peçonhentos — Aranhas, Ofídios e Escorpiões. (CIT)



TORRES, J. B. & CARLOTTO, P. R. Levantamento dos gêneros de ofídios e espécies de aracnídeos causadores de acidentes na casuística do Centro de Informação Toxicológica do Rio Grande do Sul (período compreendido entre 1977 a agosto de 1981). *Mem. Inst. Butantan*, 46:207-218, 1982.

TABELA 2

Distribuição mensal e anual dos acidentes por animais peçonhentos (Centro de Informação Toxicológica) Acidentes em humanos e animais.

Ano	1977	1978	1979	1980	1981
Mês					
Jan.	—	—	5	9	22
Fev.	—	—	6	6	23
Mar.	—	—	1	8	6
Abril	—	—	5	9	10
Mai.	—	—	4	5	17
Jun.	—	—	3	—	4
Jul.	—	—	2	1	13
Ago.	—	—	—	4	12
Set.	—	1	—	15	—
Out.	—	—	2	7	—
Nov.	—	2	8	10	—
Dez.	1	2	5	15	—
TOTAL	1	5	41	89	107

TABELA 3

Distribuição mensal de acidentes por animais peçonhentos Aranhas, Ofídios e Escorpiões. (CIT)

	J	F	M	A	M	J	J	A	S	O	N	D	TOT
Aranhas	12	15	6	10	16	3	7	10	3	2	2	8	94
Ofídios peç.	2	3	1	6	5	2	1	0	2	2	6	1	31
Escorpiões	10	7	1	0	0	0	1	0	0	0	4	6	29
TOTAL	24	25	8	16	21	5	9	10	5	4	12	15	154

TABELA 4

Percentual dos acidentes por animais peçonhentos. (CIT)

	N.º Inform.	%
Aranhas	94	61,03
Ofídios Peç.	31	20,14
Escorpiões	29	18,83
TOTAL	154	100,00

TORRES, J. B. & CARLOTTO, P. R. Levantamento dos gêneros de ofídios e espécies de aracnídeos causadores de acidentes na casuística do Centro de Informação Toxicológica do Rio Grande do Sul (período compreendido entre 1977 a agosto de 1981). *Mem. Inst. Butantan*, 46:207-218, 1982.

TABELA 5

Distribuição de ac. por Aranhas de acordo com a espécie causadora. (CIT)

	J	F	M	A	M	J	J	A	S	O	N	D	TOT
Phoneutria	2	2	1	1	4	0	4	1	0	0	1	1	17
Loxosceles	2	3	0	1	4	1	0	4	0	1	0	0	16
Lycosa	2	2	0	4	0	0	1	1	0	0	0	1	11
Caranguejeiras	0	1	0	0	0	0	0	0	0	0	0	0	1
Lactrodectus	0	0	1	0	0	0	0	0	0	0	0	0	1
TOTAL	12	15	6	10	16	3	7	10	3	2	2	8	94

TABELA 6

Percentual de acidentes por Aranhas. (CIT)

	N.º Informações	%
Phoneutria	16	35,55
Loxosceles	16	35,55
Lycosa	11	24,45
Caranguejeiras	1	2,22
Lactrodectus	1	2,22
TOTAL	45	100,00

TABELA 7

Distribuição mensal dos Ac. Ofídicos. Ofídios: Peçonhentos, Não peçonhentos e Não Identif. (CIT)

	J	F	M	A	M	J	J	A	S	O	N	D	Tot.
Ofídios Peç.	2	3	1	6	5	2	1	0	2	2	6	1	31
Of. Não Peç.	1	2	2	0	0	1	2	0	1	1	1	1	12
Não Identif.	6	2	2	1	3	1	0	4	0	1	1	3	24
TOTAL	9	7	5	7	8	4	3	4	3	4	8	5	67

TORRES, J. B. & CARLOTTO, P. R. Levantamento dos gêneros de ofídios e espécies de aracnídeos causadores de acidentes na casuística do Centro de Informação Toxicológica do Rio Grande do Sul (período compreendido entre 1977 a agosto de 1981). *Mem. Inst. Butantan*, 46:207-218, 1982.

TABELA 8

Distribuição percentual dos Acidentes Ofídicos. Segundo o gênero causador (CIT)

	N.º de Informações	%
Botrópico	27	87,10
Crotálico	2	6,45
Elapídico	2	6,45
TOTAL	31	100,00

TABELA 9

Distribuição mensal segundo o Gênero de ofídios causador de acidentes (CIT)

	J	F	M	A	M	J	J	A	S	O	N	D	Tot.
Botrópico	2	2	1	6	4	2	1	0	2	1	5	1	27
Crotálico	—	1	—	—	—	—	—	—	—	1	—	—	2
Elapídico	—	—	—	—	1	—	—	—	—	—	1	—	2
TOTAL	2	3	1	6	5	2	1	0	2	2	6	1	31

TABELA 10

Faixas etárias atingidas por Acidentes por animais peçonhentos. (CIT)

	nN	Inf. Tard	- 1 ano	1-4	5-14	15-19	20-29	30-39	40-49	50-69	+ de 70
N.º de Informações	—	—	2	29	43	16	30	20	22	21	5
%	0	0	1,06	15,4	22,8	8,52	15,9	10,6	11,7	11,1	2,65

SNAKES OF THE GUIANAN REGION

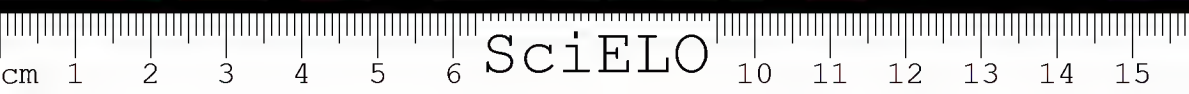
Marinus S. HOOGMOED *

ABSTRACT: The study of snakes from the Guianan region got an early start in 1705 when several species were pictured by Merian. As relatively large proportion of the snakes described by Linnaeus originated from Surinam. Interest for and knowledge of this group of animals steadily increased in the 18th and 19th century (80 species known at the turn of the century), but only in the second part of the 20 th century detailed studies of snake faunas from (part of) the Guianan region appeared. No such study for the entire area has been published till now. At present a total of 134 species of snakes, belonging to 159 taxa, is known. Only 19.4% is endemic, the majority (43.4%) belong to species with an Amazonian distribution. Seventeen species (12.7%) are venomous, ten belonging to the Elapidae, seven to the Crotalidae. Several taxonomic problems are discussed, *Cercophis auratus* (Schlegel) is restored as a valid taxon and redescribed. Analysis of available distribution data shows that forest snakes are fairly evenly distributed throughout Amazonia and Guiana. Snakes restricted to open formations are spread evenly throughout Guiana, but most of them are absent in western Amazonia. When taking together ubiquitous and snakes restricted to open formations there is a fair resemblance between the faunas of Guiana and Iquitos, but only a moderate one between Santa Cecilia and Guiana, possibly reflecting the influence of species belonging to the Andes foothill fauna (Napo refuge). Within Guiana apparently there are no unsurmountable barriers to snakes, the differences that are observed between the western and eastern/Brazilian part can be explained by the presence of species barely reaching these areas. Probably these species are still in the process of expanding their range.

INTRODUCTION

The area to be dealt with in this paper and called Guiana is the region bordered by the Rio Orinoco, the Cassiquiare Canal, the Rio Negro, the Rio Amazonas and the Atlantic Ocean (Fig. 1). This area comprises three political units in their entirety, namely Guyana (formerly British Guiana), Surinam and French Guiana. Of Venezuela it comprises the Estado Bolívar and the Territorio Federal Amazonas, known under the common denomer Guayana. Of Brasil it comprises the Territorio do

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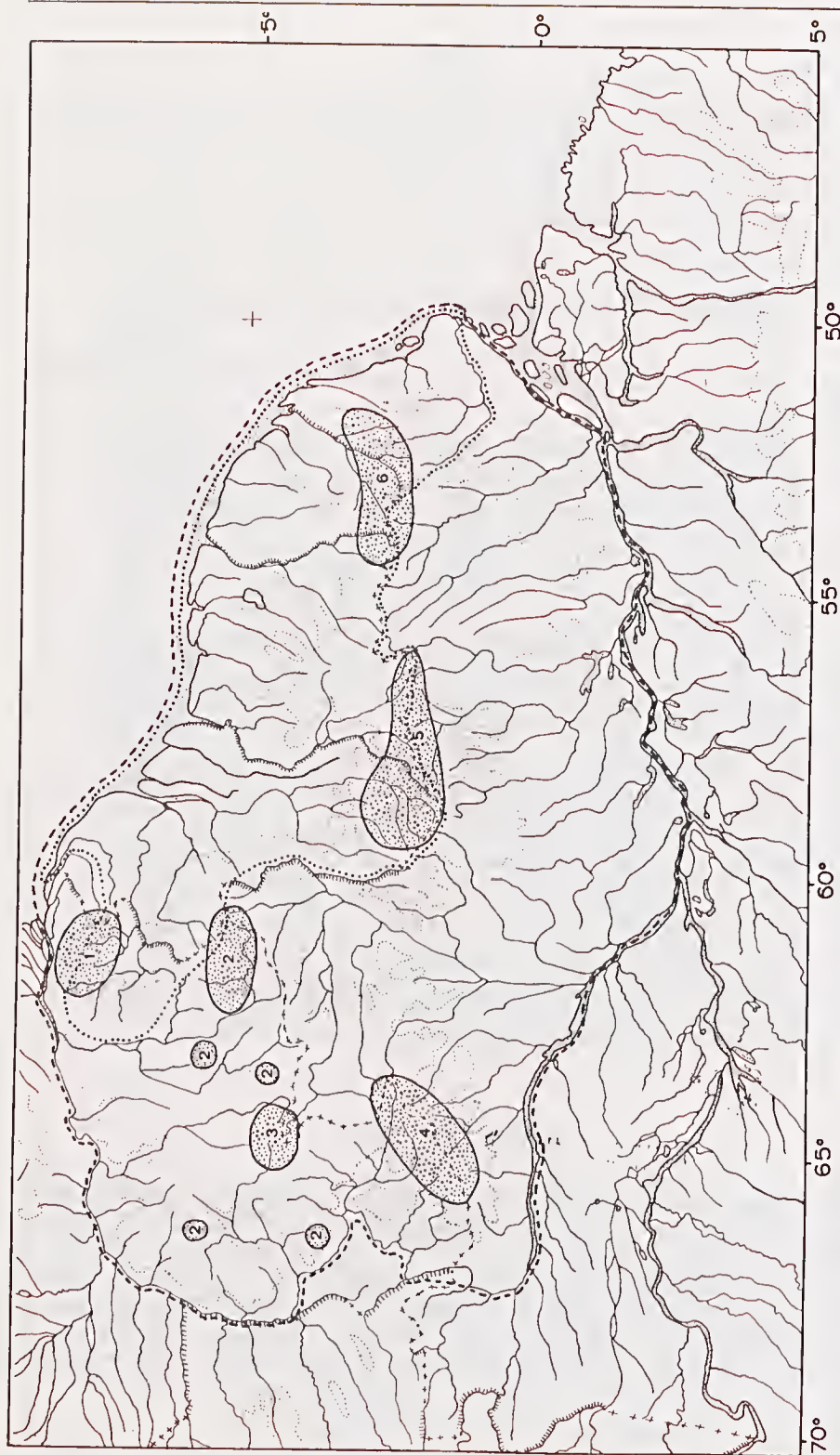


Fig. 1. Map of Guiana, showing the borders of the area as here defined (heavy broken line and as defined by Descamps et al. (1978) and by Lescure (1977) (heavy dotted line). Presumed forest refugia are gray and indicated by numbers: 1 = Imatata refuge, 2 = Korama refuge (and associated tepui refuges), 3 = Ventuari refuge, 4 = Imeri refuge, 6 = Oyapock refuge. The line of fine dots (also in fig. 4) represents the 200 m contour line.

Amapá, the Territorio de Roraima and those parts of the states of Pará and Amazonas that are situated north of the Rio Amazonas and the Rio Negro (Hoogmoed, 1979:242). French investigators (Lescure, 1977; Descamps *et al.*, 1978) tend to delimit Guiana as the area bordered by the Rio Barama (Venezuela) in the west and by the Rio Araguari (Brasil) in the southeast, the southern border being the watershed between rivers emptying directly into the Atlantic Ocean and those belonging to the Amazonian drainage. In my opinion this definition of Guiana is rather artificial and not in accordance with the biogeographical, geological and geographic data. More elaborate reasons for this rejection of the French definition are given in my 1979 paper on the herpetofauna of the Guianan region. In the same paper an extensive description of the physical features of the Guianan region is also provided (Hoogmoed, 1979:242-249).

HISTORY OF THE STUDY OF GUIANAN SNAKES

The coast of the Guianas was discovered in 1499 by Alonso de Ojeda and Amerigo Vespucci and was afterwards known as the "Spanish Main", "Wild Coast" or the "Côte Ferme". Because of tales about fabulous richness in the interior of the area many expeditions explored the region, particularly during the 16th century, in their search for El Dorado. Some of these expeditions, notably those of Sir Walter Raleigh penetrated fairly deep into the interior via large rivers like the Orinoco, but most hardly ventured inland and merely explored river mouths. It soon became evident that El Dorado either was difficult to locate, or did not exist at all, although the last possibility was only admitted reluctantly. Hence the character of the expeditions gradually changed and their main aim became the establishment of trading posts at the mouths of rivers. This process started in the second quarter of the 17th century, one of the main factors being the founding in 1621 of the "Westindische Compagnie" (West Indian Company) in the Netherlands, a trading society with interest primarily in obtaining overseas trading facilities. During part of the 17th century (1624-1654) this company even conquered a large area in northeast Brazil. The height of this conquest was during the government of Prince Johan Maurits of Nassau, who had a keen interest in science and, among his companions had scientists like Piso and Marcgraf and artists like Eckhout and Post. Their efforts must have stimulated in the Netherlands a lively interest in objects for natural history from overseas countries which led to the establishment of cabinets of natural history. Although the natural history objects collected during the Brazilian conquest were at least partly transported to the Netherlands, their present whereabouts are not known and they probably got lost. Shortly after the Brazilian episode came to an end, the Dutch settled in the coastal area of present day Surinam and Guyana. This colonisation led to an increase in traffic between Europe (mainly the Netherlands and England) and Guiana and, as a consequence, to the publication of several travelstories. Among these were the books by Warren (1667, 1669), who also paid attention to the natural history of the areas he visited. He mentioned snakes that were nearly thirty foot long. No doubt he is referring to



the anaconda, *Eunectes murinus*. The same author mentions snakes which "are knotty, with Horns in their Tails, and Tusks two Inches long upon the upper Chap". In my opinion there is little doubt he is referring to the rattlesnake of the coastal area of Surinam, *Crotalus durissus dryinus*. L. Van Berkel (1695) also refers to the rattlesnake when he describes the "Colony of Berbice" in Guyana, and to the anaconda when he is describing Surinam. However, large parts of this book have been copied from those by Warren. The first reliable pictures of snakes, which can be identified, were provided by Merian (1705a, b) in her monumental treatise on the insects of Surinam, and were painted on the spot in Surinam when she stayed there during the period 1699-1701. The species she depicted were the gardenboa *Corallus enydris* L.) (twice) and the burrowing snake *Anilius scytale* (L.). Apparently settlers and sailors provided cabinets of natural history with a steady flow of material from tropical countries. For the Netherlands this mainly involved present day Indonesia, South- and West-Africa and Surinam. The richness of these cabinets is well illustrated by Seba's monumental Thesaurus (4 volumes), in the first two volumes of which (1734/5) many snakes were illustrated. Among these snakes are at least 40 species of American provenance, even though their origin may be stated as being Cape of Good Hope or the East Indies. For several of these, Surinam is indicated as the place of origin. As the plates published by Seba were used by many subsequent writers, notably Linnaeus, for the description of species, Seba's work is of paramount importance to taxonomy. Unfortunately, of the 14 species stated by Seba to originate from either Berbice or Surinam, only seven are referable to six nominal taxa (*Boa c. constrictor* L., *Dipsas v. variegata* (D., B. & D.), *Helicops angulatus* (L.), *Leimadophis typhlus*⁽¹⁾ (L.), *Philodryas v. viridissimus* (L.) and *Oxybelis fulgidus* (Daudin). Other Guianan snakes possibly depicted by him were *Liophis cobella* (L.) and *Drymoluber dichrous* (Peters). The remainder either is unidentifiable on the basis of the drawing and the description, or could be interpreted in several ways. Many of the other figured South American snakes also occur in Surinam and probably originate from that country as well. Seba's first collection was sold to Czar Peter the Great and subsequently got lost for the greater part. His second collection was auctioned 16 years after his death in 1752 and part of it now is in the Zoological Museum in Leningrad (Juriev, 1981). Unfortunately I could not yet examine that material and solve some of the remaining problems.

Another important contribution to our knowledge of Guianan snakes was made by Scheuchzer (1735a, b, 1738) in his *Physica Sacra*. In this work he depicted a number of snakes from the collection of J. H. Linck, a pharmacist with a famous cabinet in Leipzig. The drawings were well done and most of them can be identified relatively easily. The snakes were generally drawn life size and apparently in the position they were

(1) Throughout this paper I have adopted the generic names *Leimadophis*, *Liophis* and *Lygophis* as used by Peters & Orejas-Miranda (1976), although I am fully aware of the studies that have been going on recently in this group of related genera. The most recent paper dealing with this subject is that by Dixon (1980), who classified all species belonging to these genera as *Liophis*. Although I sympathise with his views and accept his arguments I did not adopt his classification here, because this would have included too many alterations in the manuscript of this paper. I did, however, use some of his as yet unpublished results, which are acknowledged as "personal communication".

preserved in. Thus, in many cases it is possible to reconstruct the glass jars they were stored in by taking a ruler and a pair of compasses and drawing a few tangent lines. This to illustrate the exactness with which the drawings were executed, much more accurately depicting the actual specimens than those in the famous work of Seba. The largest part of the snakes depicted and rather superficially, described (47 of 64) apparently originated from South America and of these 47, ten were stated to come from Surinam. For two of these (*Cylindrophis rufus* (Laur.) and *C. maculatus*, (L.) both from Southeast Asia), the locality obviously is in error, the other eight do occur in Surinam. Amongst the species reported by Scheuchzer for the first time from the Guianan region are *Erythrolamprus a. aesculapii* (L.), *Leptophis a. ahaetulla*, (L.) *Lygophis l. lineatus* (L.), *Oxybelis argenteus* (Daudin), *Oxyrhopus p. petola* (L.) and *Rhinobothryum lentiginosum* (Scopoli). Scheuchzer's work also was frequently referred to by subsequent writers, like for instance Gronovius (1756), and its importance for herpetology may be illustrated by the history of the name *Coluber jaculatrix* Linnaeus, 1766, still cited by Peters & Orejas-Miranda (1970) with a questionmark in the synonymy of *Lygophis l. lineatus* (L.). This was based only on the inclusion of the references to it in Lacépède and Latreille in the synonymy of this species as presented by Hoge (1952). However, the matter is relatively simple: Linnaeus (1766) referred to species n.o 26 of Gronovius (1756), who in turn referred to Scheuchzer (1735b), plate 715 fig. 2 and provided a fairly good description. Combining these data it is evident that *Coluber jaculatrix* Linnaeus, 1766 is a synonym of *Lygophis lineatus* (Linnaeus, 1758). Therefore the importance of Scheuchzer's work for herpetology should not be neglected. Unfortunately the present whereabouts of the material from Lincke's cabinet is not known. Apparently it is not in one of the museums in the DDR (Peters, Obst, personal communications).

Sundius (1749), contributing to Linnaeus's (1749) *Amoenitates Academicae*, described ten species of snakes from Surinam, all but one of which can be identified. He added *Thamnodynastes pallidus* (L.) and *Micrurus lemniscatus* (L.) to the list of snakes known from the Guianan region. Gronovius (1756), in describing his own collection, mentioned 18 species of snakes from Surinam, of which four actually come from Southeast Asia one from Europe, three are unidentifiable and ten could be identified as Guianan snakes, of which *Leptodeira a. annulata* (L.) *Philodryas olfersii herbeus* (Wied) and *Thamnodynastes strigilis* (Thunberg) constitute new faunal records. Linnaeus (1758) based himself on material present in Swedish collections of which a large proportion either had been obtained by purchase from the Netherlands (among others part of the Seba collection was acquired for the king of Sweden), or had been collected by Rolander, one of Linnaeus pupils, in Surinam, or apparently had come from Surinam through the Netherlands along other channels. In the 10th edition of his *Systema Natura* Linnaeus only mentioned three species as coming from Surinam, but in his synonymies he included many references to Surinam species described by Sundius, Gronovius and Seba. In Houttuyn's so-called Dutch edition of Linnaeus's *Systema Natura* (1764), which was only partly a translation and primarily an elaboration based on material in his own collection and that



of e.g., Gronovius, a total of 12 snakes was stated to have come from Surinam. Two of these are of Southeast Asian provenance, the other ten indeed are from Surinam. Houttuyn added two more species to the known snake fauna of the Guianas, viz. *Typhlops reticulatus* (L.) and *Corallus caninus* (L.). It seems useful to indicate here that the description of *Typhlops reticulatus* by Linnaeus was based on two descriptions and a plate in older literature and that he himself apparently did not have any material of this species available. His synonymy included a reference to Scheuchzer's (1735b) plate 747 fig. 4 and to Gronovius's description of his seventh species, the *Anguis* with 177 ventrals and 37 subcaudals. The first reference is correct (Dixon & Hendricks, 1979), the second, however, is not. After long deliberations both Dixon and I came independently to the conclusion that Gronovius did not describe *Typhlops reticulatus* but in fact was referring to *Amphisbacna fuliginosa* L., a wormlizard. By selecting RMNH 7660 as the neotype, Dixon & Hendrick (1979) stabilised the nomenclature of *Typhlops reticulatus*.

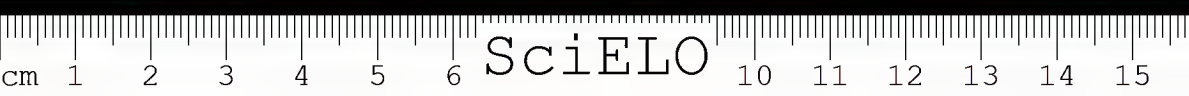
Barrère (1741) in his popular account of the natural history of French Guiana mentioned several species of snakes from that country, of which only one, *Crotalus durissus* L., is identifiable.

Fermin (1765) and Hartsinck (1770) gave popular accounts of the natural history of Surinam, but most of the snakes they mentioned are difficult to identify. Linnaeus (1766), Laurenti (1768), Linck (1783) and Gmelin (1789) did not add any new species to the list of known Guianan snakes. Until the end of the 18th century nearly all material of Guianan snakes came from Surinam, which in this context should be widely interpreted as comprising also eastern Guyana (Berbice and Demerara). In 1802 Latreille (1802a, b) reported several snakes from French Guiana, comprising the most common species like *Boa constrictor*, anaconda and rattlesnake. Daudin (1803a-d) in his "Histoire naturelle... des reptiles" presented a nearly complete compilation of the snakes at that moment known from the Guianan region, most still only recorded from Surinam, but also some species that had become known from French Guiana or Cayenne (as the colony sometimes also was called, in reference to its capital). Only three species formerly known from the area under consideration were not included in Daudin's compilation. On the other hand he reported five species new for the region, of which *Sibon ncbulata* (L.) and *Pseudoeryx plicatilis* (L.) were already known to science, the other three (*Clelia c. clelia* (Daudin), *Tripanurgos compressus* (Daudin) and *Micrurus psyches* (Daudin)) were described here for the first time. Fitzinger (1826), basing himself on the literature, added three species which had been described recently (*Leimadophis poecilogyrus amazonicus* Amaral, *Xenodon severus* (L.) (including *X. aeneus* Boie from Surinam in its synonymy) and *Micrurus s. surinamensis* (Cuvier)).

Our knowledge of Guianan snakes spectacularly increased by the publication of Schlegel's (1837) "Essaie sur la physionomie des serpens". This book was mainly based on the rich collections of the Rijksmuseum van Natuurlijke Historie in Leiden, Netherlands which in the eighteen twenties and thirties had in Surinam a very active collector, the pharmacist H. H. Dieperink, who regularly sent large consignments of pre-



served material to Leiden (Holthuis, 1959). Moreover, Schlegel had good contacts with the Paris herpetologists Duméril and Bibron and also used part of the collections of the Paris museum. From this time on snakes from other areas within Guiana became known in growing numbers. Through Schlegel's efforts in 1837 a total of 54 snakes was known from Guiana. It might become boring to mention all the 21 species added to the Guianan snake-fauna by Schlegel, but I wish to record here four which Schlegel described for the first time. They include *Dipsas pavonina* Schlegel and *Dendrophidion dendrophis* (Schlegel), both based on specimens from French Guiana, and *Pseustes sulphureus dieperinkii* (Schlegel) and *Cercophis auratus* (Schlegel), both described from Surinam and both with a confused history. The allocation of *Dipsas Dieperinkii* Schlegel, 1837 was cleared by Brongersma (1937), who considered it a synonym of *Pseustes s. sulphureus* as used by Amaral (1930), and by Hoge & Romano (1969) who considered it a distinct subspecies of *Pseustes sulphureus* (Wagler). *Dendrophis aurata* Schlegel, 1837 never has been allocated properly until now, possibly because it was confused with Schlegel's *Dryiophis auratus*, a synonym of *Oxybelis aeneus* (Wagler). The species was described on the basis of a single specimen from Surinam, collected there by Mr. Dieperink. The species served Fitzinger (1843) as type of his genus *Cercophis*. Duméril, Bibron and Duméril (1854) did not know where to place it and did not pursue the matter. As far as I am aware, the species was only cited by Schlegel (1858), it was not mentioned by Günther (1858) or by Boulenger (1893, 1894, 1896) in their Catalogues of Snakes in the British Museum, nor by Amaral (1930) or Peters & Orejas-Miranda (1970) in their respective checklists of South-American snakes. Romer (1956:580) considered *Cercophis* a junior synonym of *Oxybelis*. Keiser (1974), acting in accordance with my advice, did not include *Dendrophis aurata* Schlegel, 1837 in the synonymy of *Oxybelis aeneus* (Wagler). I did investigate the type-specimen (RMNH 813), which unfortunately is in a rather poor condition (e.g. the epidermis has largely disappeared) but still good enough to allow taxonomic conclusions. In my opinion this species, described by Schlegel (1837) and made the type of a new genus by Fitzinger (1843), is completely different from any other known South American snake and therefore properly should be called *Cercophis auratus* (Schlegel, 1837). It can be recognised by a combination of the following characters: scales on the back smooth, without pits, arranged in 15-15-11 longitudinal rows, of which the vertebral one is enlarged, ventrals (140) fewer than the subcaudals (163), which are paired, anal divided, a very long slender body and tapering tail, with the thickest part of the body just anteriorly to the cloaca, head small, distinctly wider than the neck, mandibular teeth subequal, maxillary teeth 20 followed by two enlarged, solid teeth, separated by a diastema from the preceding teeth. Scalation of the head (Fig. 2): one pre- and two postoculars, a small, rectangular loreal, temporals 1+2, eight supralabials, fourth and fifth bordering the eye, ten infralabials, five of which are in contact with the anterior pair of chinshields. This does not seem the place to speculate on the proper position of this species within the Colubrids, that would ask for more and preferably recently collected material to provide us with much needed additional information on the osteology. However, most likely this is a member of the Xenodontinae.



Cercophis auratus (Schlegel, 1837)
RMNH 813 holotype

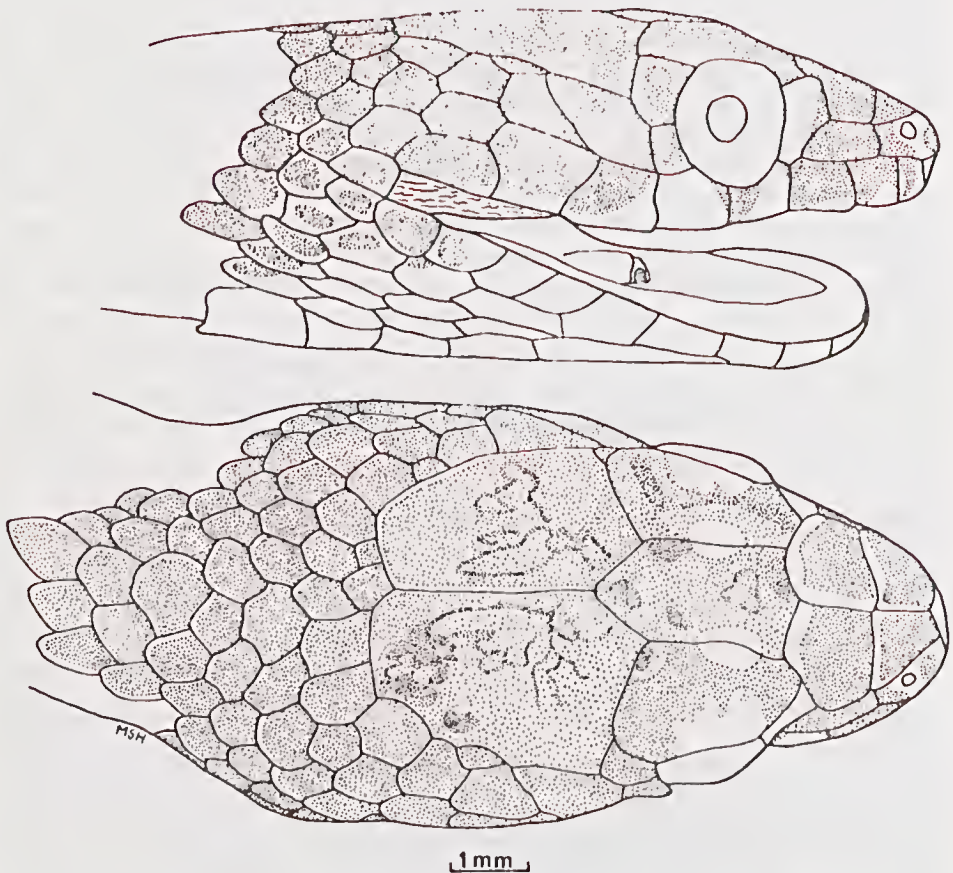


Fig. 2. *Cercophis auratus* (Schlegel), lateral and dorsal view of head of holotype, RMNH 813.

The first paper dealing with the reptiles and amphibians of British Guiana (Troschel, 1848) increased our knowledge of Guianan snakes by adding five more taxa to the list. Among these were *Phimophis guianensis* (Troschel), new to science, and the first mention of *Crotalus durissus ruruima* Hoge. This rattlesnake was considered as one species throughout British Guiana, but specimens from the coastal savannas (*C. d. dryinus* (L.)) and from the surroundings of Mount Roraima on the border of Guyana, Venezuela and Brazil (*C. d. ruruima* Hoge) were separately mentioned. Although the monumental work of Duméril, Bibron & Duméril (1844, 1854) was a land-mark in the history of herpetology, it did not substantially contribute to our knowledge of Guianan snakes, because this work only added six more taxa to the list. Two taxa (*Dipsas v. variegata* (D., B. & D.) and *Atractus torquatus* (D., B. & D.)) which were (validly) described here for the first time, had previously been reported from

the region by respectively Seba (1735) and by Schlegel (1837) (in the synonymy of this composite *Atractus badius*). Another one (*Ablabes purpurans*) falls into the synonymy of *Liophis miliaris* (L.) (Dixon (1978)), personal communication). Of the six taxa reported for the first time from Guiana none were new to science. One of these species (*Typhlophis squamosus* (Schlegel) had been reported from Cayenne in the original description, but had not yet been included in general works used to compile the present survey. Minor additions to the list of Guianan snakes were made by Günther (1858) (with whose data I combined Gray's (1849)), Jan & Sordelli (1860-1881), Kappler (1885), Boulenger (1893, 1894, 1896) and Van Lidth de Jeude (1898, 1904, 1917). Amaral's (1930) checklist, based upon a survey of the literature added another ten taxa, bringing the total up to 91. Roze (1966) compiled the data on Venezuelan snakes and enlarged the total to 116 by adding to the list 25 new taxa, which were mainly based on the extension of known ranges into the Guianas, on the splitting of formerly monotypic taxa, and to a large proportion (about 1/3) on the description of several new taxa by Roze. The checklist by Peters & Orejas-Miranda (1970) compiled most known data on South American snakes and listed a total of 135 from the Guianas. Hoogmoed (1979) gave a summary of the available information, combining literature data with those from his own research and from fieldnotes, mainly on Surinam snakes. At approximately the same time, Lancini's (1979) book on Venezuelan snakes appeared and together they increased the known number of snake taxa in Guiana to 157. Gasc & Rodriguez (1980b) dealt with the snakes of French Guiana mainly on the basis of recently collected material and listed for this country a total of 77 taxa (one of which was mentioned only in the general discussion). Unfortunately they did not sufficiently take into account the old literature and their list is far from complete. They (1979) described as new *Atractus zidoki*, which had also been reported by Hoogmoed (1979) as *Atractus* sp. A, and in another paper (1908a) *Geophis alasukai*, which is a junior synonym of *Atractus flammigerus* (F. Boie).

Summarizing, we can say that since the end of the last century the number of snake-taxa known for the region doubled. Thus, in the past 85 years an equal number of taxa became known as in the previous 229 years.

The gradual increase and present state of our knowledge about Guianan snakes is reflected in the graph (Fig. 3) and in the appendix 1 which include 159 nominal taxa.

Differences with the list provided by Hoogmoed (1979) are the result of diverse causes:

1. Oversight of previous literature records.
2. Descriptions of new taxa and new locality data.
3. Identifications of hitherto questionable taxa and re-identifications.
4. Revisions of genera.
5. Hoogmoed (1979) only listed full species, subspecies were not taken into account.





Fig. 3. Graph showing increase in knowledge about Guianan snakes. Dates refer to publications listed in caption of Appendix.

1. Among the first group are *Cercophis auratus* (Schlegel), *Waglerophis merremii* (Wagler) and *Leptomicrurus schmidti* Hoge & Romano, for which definite Guianan localities are known (Schlegel, 1837; Boulenger, 1894 and Gasc & Rodrigues, 1980b; Hoge & Romano, 1966). *Pliocercus euryzonus euryzonus* Cope has been reported from Amazonian Brazil, but it is not clear whether it really does occur in the Guianan region or just comes close to it. For completeness sake it has been included here.

2. The second group comprises among others *Typhlops minuisquamus*, recently described by Dixon & Hendricks (1979), and *Atractus zidoki*, described by Gasc & Rodriguez (1979), previously reported as *Atractus* sp. A by Hoogmoed (1979). In this group also should be included *Eunectes deschauenseci* Dunn & Conant, formerly known from Isla Marajó only, but recently reported from eastern French Guiana, from swamps near the river Approuage, by Matz & Matz (1981), who substantiated their report with colour-photographs of living specimens. Hereby the known range of this species is considerably extended to the northwest and follows a pattern of distribution well known for several other reptiles and amphibians inhabiting marshy areas in the lower Amazonian region (*Crocodilurus lacertinus* (Daudin), *Peltocephalus tracaxa* (Spix), *Melanosuchus niger* (Spix) and *Hydrolaetare schmidti* (Cochran & Goin). *Masticophis mentovarius suborbitalis* (Peters) recently was reported from the northwestern part of the Guianan region by Lancini (1979), whereas Wiest (1978) reported *Chironius m. multiventris* Schmidt & Walker from the extreme southern edge. Harris & Simmons (1978) described the new subspecies *Crotalus durissus trigonicus* from the Rupununi savanna in southern Guyana.

Bothrops eneydae Sandner Montilla is only hesitantly included in the list of Guianan snakes on the basis of the fact that Hoge & Romano Hoge (1981) included it in their checklist of poisonous snakes of the world. However, I did not yet have the opportunity to examine the original description, or the holotype, which apparently already got lost (Sandner Montilla, 1981, personal communication). Personally I have my strong doubts about the validity of this species, but until further information becomes available it is retained on the list.

3. A number of hitherto questionable identifications could be corrected, either in generic revisions or because additional material became available for study. Thus, the following synonymies for names in Hoogmoed (1979) can be listed:

Leptotyphlops sp. A = *Leptotyphlops amazonicus* Orejas-Miranda

Chironius sp. A = *Chironius exoletus* (L.)

Chironius bicarinatus = *Chironius exoletus* (L.)

Chironius cinnamomeus = *Chironius scurrulus* (Wagler)

Oxyrhopus sp. A = *Oxyrhopus formosus* (Wied)

Liotyphlops incertus Amaral = *Liotyphlops ternetzii* (Boulenger)

Aporophis crucifer Ahl = *Leimadophis melanotus* (Shaw)

Liophis purpurans (D., B. & D.) = *Liophis miliaris* (L.)



These synonymies need some explanation. *Leptotyphlops* sp. A was identified as *L. amazonicus* on the basis of material seen in Venezuelan museums and collected during field-work in Venezuela in 1978. *Chironius* sp. A was identified as *C. exoletus* and *C. cinuamomeus* as *C. scurrulus* on the basis of the revision of the genus *Chironius* by Wiest (1978). *C. bicarinatus* from Guiana (Hoogmoed, 1979:275) was based on a number of specimens seen by me in 1975 in collections in French Guiana (SEPANGUY, Institut Pasteur) and Surinam (Surinaams Museum), without access to literature and insufficient material for comparisons. The specimens compared well with specimens of *C. bicarinatus* (Wied) from Brazil present in these collections, and were tentatively identified as such. However, upon consulting Wiest (1978) it soon became evident that in reality they belong to *C. exoletus*. Thus, the record in Hoogmoed (1979) of *C. bicarinatus* occurring in Guiana is based on a misidentification. *Oxyrhopus* sp. A was identified as *O. formosus* on the basis of recently collected additional material while taking into account the remarks made by Gasc & Rodrigues (1980). According to Mr. C. P. Kofron (1979, personal communication), *Liotyphlops incertus* identical with *L. ternetzii*, a species formerly known from southern Brazil, Paraguay and northern Argentina, but recently reported from the area around Belém by Da Cunha & Do Nascimento (1975). I investigated the holotype of *Apovophis crucifer* in the Berlin museum and came to the conclusion that it is identical with *Leimadophis melanotus*. According to Dixon (1978, personal communication) *Liophis purpurans* is a synonym of *L. miliaris*.

4. *Typhlops unilineatus* has been omitted from the list, because according to Dixon & Hendricks (1979) this probably is an oriental species.

A partial revision of the genus *Atractus* (Hoogmoed, 1980) led me to consider *A. micheli* Mocquard and *A. subbicinctum* (Jan) (the latter name not mentioned by Hoogmoed, 1979) as synonyms of *A. badius* (F. Boie). Also it turned out that two names considered synonyms of *A. badius* since 1837 were good species (*A. flammigerus* (F. Boie), *A. schach* (F. Boie)), well differentiated from *A. badius* in scale characters, hemipenial morphology and colour pattern. Consequently these names were restored to species level. Gasc & Rodrigues (1979), at approximately the same time, described a new species, *A. zidoki*, from French Guiana, which also had been discovered in Surinam. *Geophis alasukai* from French Guiana was described by Gasc & Rodrigues (1980a), who paid much attention to this unexpected find and devoted quite a discussion to the supposed relationships of this taxon with species of the group *omiltemanus* in Mexico. The very strange distribution indeed was explained away as being the result of an ancient wide distribution having been interrupted due to vegetational changes as a result of climatic fluctuations. Examination of the types of *Geophis alasukai* convinced me that it actually is identical with *Atractus flammigerus*. However, I must add that the genus *Atractus* is in a state of confusion as becomes evident rapidly when studying species belonging to this genus. Lack of material of many species is one of the main factors frustrating thorough taxonomic work on this group. From the papers by Hoogmoed (1980) and Gasc & Rodrigues (1979, 1980a) it is evident that a revision of the genus is highly



desirable and that it should pay much attention to hemipenial morphology, scale structure, body proportions and osteology. Until such a revision is made hypotheses about relationships within this group and about its zoogeographic affinities remain highly speculative.

5. Whereas Hoogmoed (1979) only listed species, in the present paper subspecies have been taken into account as well, establishing the total number of taxa. It would lead us too far afield to consider these differences in detail here.

Some of the identifications leading to my present estimate of 159 snake-taxa for the Guianan region are not beyond doubt as has already been suggested above in the case of taxa either just or not reaching Guiana. However, there are some other problems as well. For instance, *Chironius scurrulus*, as used by me, may be a composite of two taxa, either species or subspecies. In this connection I may refer to the description and pictures of this species in Lancini (1979), which closely agree with those in Wagler (1824), while all describe the species as being reddish brown with dark spots, having a lighter belly with darker spots. Specimens (juveniles, halfgrown, adults) I have investigated from Surinam, Peru and Bolivia agree in all scale characters with the description of *C. scurrulus*. However, they differ in colour by being immaculately grey-green. The taxonomic consequences of this observation are not yet clear, but investigation of the holotype showed that *Dendrophis viridis* D., B. & D., 1854 constitutes a synonym of the green form and is not a synonym of *Chironius fuscus* (L.) as Peters & Orejas-Miranda (1970) thought. Boulenger (1894) treated the green form as a separate variety B. of his *C. fuscus*. Both Duellman (1978) and Dixon & Soini (1977) reported the juveniles of *C. scurrulus* to be leaf-green with a gradual change to a mottled brown pattern in adults. Wiest (1978:249) synonymised *D. viridis* with *C. scurrulus* and attributed the colour differences to ontogenetic changes, juveniles being green, adults having various colours, ranging from yellow to black. He also pointed out that the name *C. cinnamomeus* was used by recent authors (Hoge, 1964; Peters & Orejas-Miranda, 1970 (and also Hoogmoed, 1979) for reddish brown or cinnamon coloured specimens of *C. scurrulus* and that *Natrix cinnamomea* Wagler possibly is a synonym of *Pseustes poecilonotus polylepis* (Peters). During a recent study of Spix and Wagler type specimens in the Zoologische Staatssammlung München (Hoogmoed & Gruber, in preparation), one of the syntypes of *Natrix scurrula* Wagler (ZSMH 2628/0) was located, so contrary to what Wiest (1978:249), who actually examined the specimen, and Hoge & Do Maranhão Nina (1964:74) were led to believe, apparently not all type material of this species was destroyed in World War II.

Another problem is posed by the species of *Thamnodynastes*. In Guiana two species occur: *T. pallidus* (L.) with an entire anal, smooth dorsal scales without apical pits, arranged in 17-17-13 rows, 137-160 ventrals, 82-90 paired subcaudals, an entire nasal and a relatively large, orange eye, and another species with divided or undivided anal, smooth dorsal scales which have only one indistinct apical pit, arranged in 19-19-15 rows, 137-150 ventrals, 62-75 paired subcaudals, a semidivided nasal and a relatively small, brown eye, whose identification is somewhat more complicated. Using the key provided by Peters & Orejas-Miranda



(1970) this species keys out as *T. strigatus* (Günther), a species from southern Brazil. However, in males of the Guiana-form there are no supra-anal tubercles as in *T. strigatus*, moreover they do agree fairly well with the description of *T. strigilis* (Thunberg), known from the area with keeled dorsal scales (see e.g. Lancini, 1979, fig. 60), and I tentatively identified them as *T. strigilis*. So either *T. strigilis* has smooth scales in certain populations (already indicated by Boulenger (1885) when he described *Thamnodynastes Nattereri* var. *laevis*), or *T. strigatus* reaches the Guianan region as well, or the taxon here tentatively called *T. strigilis* is a new species. Dr. Bailey is actively working on these problems, so I may refer to his paper in this volume.

ZOOGEOGRAPHY

At present 159 snake-taxa belonging to 135 species are known to occur in the Guianan region. Of these, 29 taxa, belonging to 17 species are venomous snakes of the families Elapidae and Crotalidae. The remainder belong to the families Anomalepidae, Leptotyphlopidae, Typhlopidae, Aniliidae, Boidae and Colubridae (table 1).

TABLE 1
Families of Guianan snakes

	taxa	species
Anomalepidae	2	2
Leptotyphlopidae	7	7
Typhlopidae	4	4
Aniliidae	2	1
Boidae	9	6
Colubridae	106	98
Elapidae	18	10
Crotalidae	11	7
	159	135

When trying to make a zoogeographic analysis of the Guianan region we should realise that there are widely diverse ecological conditions within the confines of Giana. The altitude of the region varies from sea-level to nearly 3000 m, and consequently there are differences in vegetation related to the altitude. Vegetationtypes to be encountered range from tropical lowland rainforest and savanna forest to montane forest, cloud forest and mangrove forest, from lowland savanna to altitudinal savanna and also include lowland swamp and riverine forest. Especially the savannas play an important role in the distribution of certain organisms in South America, by either acting as barriers or as dispersal



routes, depending on the ecological preferences of the organism involved. They are mainly situated in the western part of Guiana, where they connect with the llanos of Central Venezuela; in the northern, coastal area of the Guianas and Amapá, and in the interior, in the area forming a diagonal band from northwest to southeast, coinciding with a zone of lower annual precipitation (figs. 4, 5). During the past decade or so, the hypothesis has been postulated (Haffer, 1969, 1979; Van der Hammen, 1974) that under the influence of climatic fluctuations in the Pleistocene and Holocene the vegetation responded by exhibiting more or less simultaneous contractions and expansions. During dry climatic phases the savannas would expand, and the forest would retract to refuge-areas in climatically favoured (= relatively wet) areas, thus offering good opportunities for the extension of savanna-inhabiting species. During wet climatic phases the opposite would occur, the forest would expand again and the savannas would retract to relatively dry areas with unfavourable edaphic factors. Since its propagation this hypothesis has been used to explain quite satisfactorily distribution patterns of several groups of animals and plants in South America. For the rattlesnake *Crotalus durissus*, a savanna-inhabitant, and also for the rainforest-inhabitant *Lachesis muta*, the bushmaster (fig. 6), the hypothesis offers a good explanation for the facts as we observe them today. During dry climatic phases the original stock of *Crotalus durissus* was able to spread through lowland South America from Central America. During wet phases different populations became isolated and presently can be recognised as different subspecies e.g. in Guiana there are four subspecies known: *C. d. cumanensis* Humboldt in the northwestern part of the area, *C. d. dryinus* L. in the coastal savannas, *C. d. ruruima* Hoge in the border area between Brazil and Venezuela and *C. d. trigonicus* Harris & Siimmons on the Rupununi-savanna in Guyana.

Forty five species of Guianan snakes are known to occur on savannas or in comparable habitats like open, grassy swamps (table 2). Twenty four of these are restricted to this habitat, the others may be found in rainforest or in edge-situations as well. The remaining species are inhabitants of rainforest, montane forest or cloud forest. However, our knowledge about the ecological requirements of snakes within the forest or the savanna is very limited. Nevertheless, the main patterns are evident and we can use that knowledge in the zoogeographical analysis.

According to their distribution the snakes of the Guianan region can be grouped into several assemblages. Hoogmoed (1979) discerned eight main distribution patterns, which were partly subdivided, to yield 12 patterns, for the entire herpetofauna. Gasc & Rodrigues (1980b) distinguished five for snakes in French Guiana and Duellman (1978) recognised eight in the herpetofauna of Santa Cecilia in Ecuador, of which five involve Guianan species as well. The establishment of distribution patterns is important to answer questions about the origin of the present fauna and it may also serve to solve the question of how the fauna reached the region. As stated above, a factor limiting the possibilities of interpretation is our scant knowledge of the ecological requirements of snakes, many of which are only known from one or a few specimens.

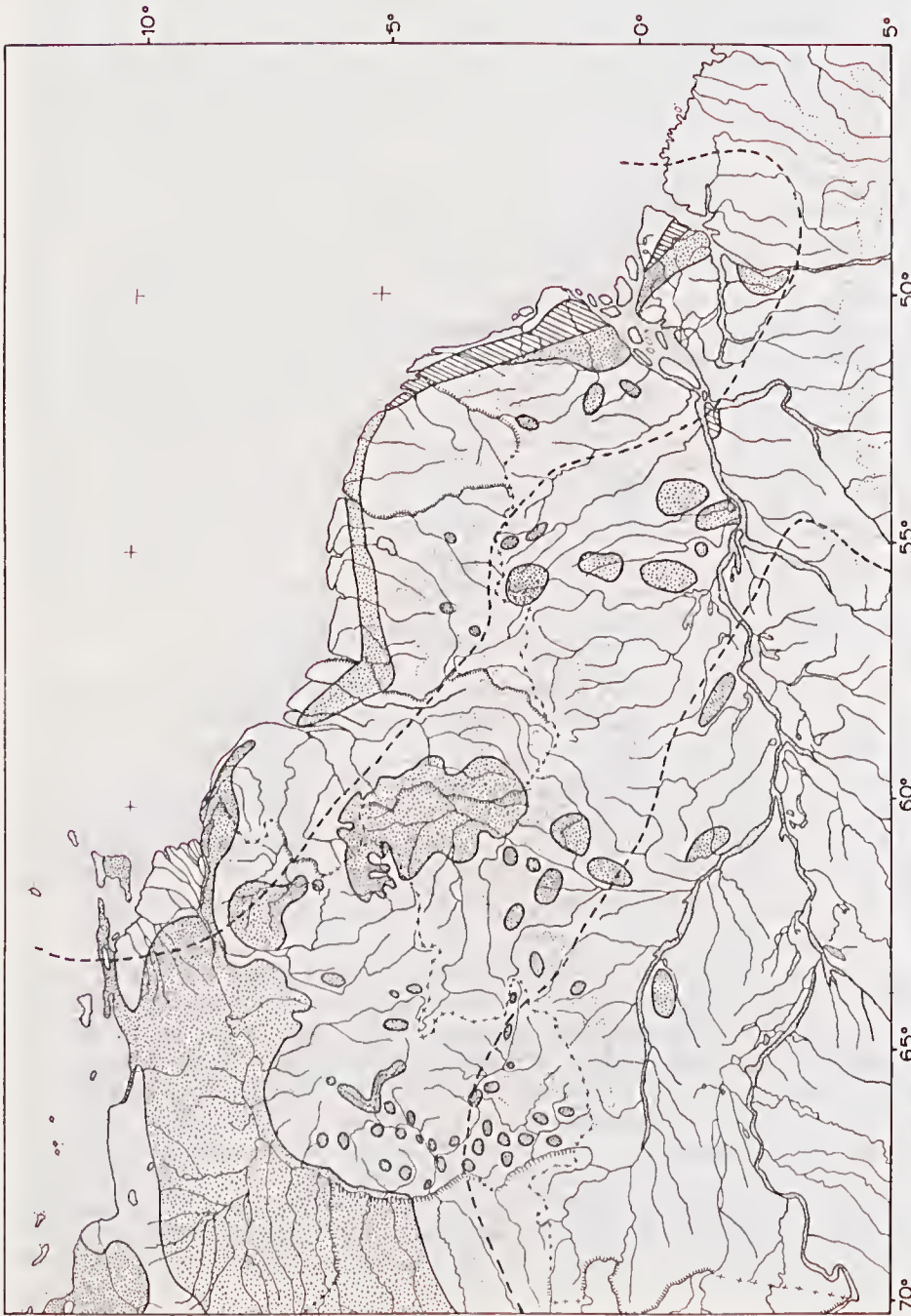


Fig. 4. Map of Guiana showing the distribution of forest and savannas. Forested areas white, inundated savannas hatched, savannas stippled. The zone with lower rainfall (cf. fig. 5) has been indicated with heavy broken lines (after Hoogmoed, 1979).

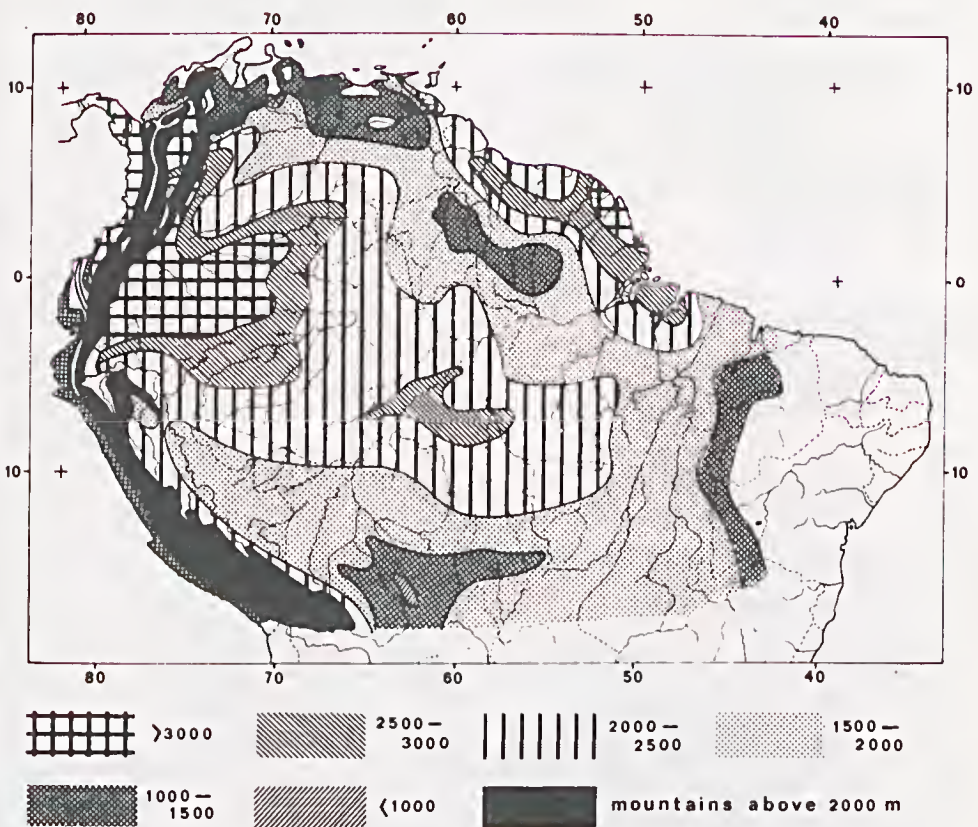


Fig. 5. Rainfall (mm) distribution in northern South America (after Hoogmoed, 1979).

Of the groups discerned by Hoogmoed (1979), the ones comprising wide-ranging cosmopolitan species, species with uncertain distributions and species with disjunct populations in Upper Amazonia and near the mouth of the Rio Amazonas, do not include any snakes. Twenty five species from regions as far apart as Europe, South Africa, Indonesia and the Antilles have been reported from Guiana, all demonstrably based on wrongly labelled material and consequently not considered in the present compilation (appendix). Only one species of snake (*Typhlops lumbricallis* (L.)) has apparently successfully been introduced into Guyana from the Antilles. The remaining 134 species can be grouped as follows (table 2, figs. 7, 8, 9) :



TABLE 2

Guianan snakes arranged according to their distribution (see text for further explanation). Species restricted to open formations (mostly savannas) are indicated with a +, species occurring in open formations, in forest and in edge-situations (ubiquists) are indicated with a °. Species without a mark are considered as strictly forest species, which may however occur in forest-edges.

1A. Altitudinal endemics: 6 species, 4.5%.

- | | |
|-------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <ul style="list-style-type: none"> <i>Atractus duidensis</i> Roze + <i>rivcroi</i> Roze + <i>Liophis ingeri</i> Roze | <ul style="list-style-type: none"> <i>Liophis trebbau</i> Roze + <i>Thamnodynastes chimanta</i> Roze + <i>Bothrops cneydae</i> Sandner Montilla |
|-------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

1B. Lowland endemics: 20 species, 14,9%.

- | | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <ul style="list-style-type: none"> + <i>Leptotyphlops amazonicus</i> Orejas-Miranda + <i>collaris</i> Hoogmoed + <i>dimidiatus</i> (Jan) + <i>septemstriatus</i> (Schneider) + <i>Eunectes aëschauensei</i> Dunn & Conant <i>Dipsas copei</i> (Günther) <i>Apostolepis quinquelineata</i> Boulenger <i>Atractus favae</i> (Filippi) <i>insipidus</i> Roze <i>schach</i> (F.Boie) | <ul style="list-style-type: none"> <i>Atractus steyermarki</i> Roze <i>trilineatus</i> Wagler <i>zidoli</i> Gasc & Rodrigues <i>Cercophis auratus</i> (Schlegel) <i>Helicops hoyei</i> Lancini <i>Liophis canaima</i> Roze <i>Xenodon werneri</i> Eiselt <i>Leptomicrocrurus collaris</i> (Schlegel) <i>schmidti</i> Hoge & Romano <i>Micrurus averyi</i> Schmidt |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

2A. Periferal amazonian: 12 species, 9%.

- | | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <ul style="list-style-type: none"> <i>Atractus latifrons</i> (Günther) <i>Drepanoides anomalus</i> (Jan) <i>Drymohuber dichrous</i> (Peters) <i>Imantodes lentifrus</i> (Cope) <i>Liophis breviceps</i> Cope <i>undulatus</i> (Wied) | <ul style="list-style-type: none"> <i>Ninia huásoni</i> Parker <i>Pseudoboa coronata</i> Schneider + <i>Thamnodynastes pallidus</i> (L.) <i>Xenopholis scalaris</i> (Wucherer) ° <i>Micrurus lemniscatus</i> (L.) <i>psyches</i> (Daudin) |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|

2B. Amazonian basin: 5 species, 3.8%.

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|------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------|
| <ul style="list-style-type: none"> <i>Helicops hagmanni</i> Roux <i>polylepis</i> Günther <i>trivittatus</i> (Gray) | <ul style="list-style-type: none"> <i>Hydrops martii</i> (Wagler) <i>Rhadinea brevirostris</i> (Peters) |
|------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------|

2C. Wideranging amazonian: 41 species, 30.6%.

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|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <ul style="list-style-type: none"> <i>Leptotyphlops tenella</i> Klauber <i>Typhlops brongersmianus</i> Vanzolini <i>reticulatus</i> (L.) <i>Anilius scytale</i> (L.) <i>Corallus caninus</i> (L.) ° <i>Eunectes murinus</i> (L.) ° <i>Dipsas catesbyi</i> (Santzen) <i>indica</i> (Laurenti) <i>pavonina</i> Schlegel <i>Atractus badius</i> (F.Boie) <i>flammigerus</i> (F.Boie) | <ul style="list-style-type: none"> <i>Leimadophis typhlus</i> (L.) ° <i>Liophis cobella</i> (L.) + <i>Mastigodryas bifasciatus</i> (Raddi) ° <i>boddacerti</i> (Santzen) <i>Oxybelis argenteus</i> (Daudin) <i>Oxyrhopus formosus</i> (Wied) + <i>Philodryas olfersii</i> (Lichtenstein) <i>viridissimus</i> (L.) ° <i>Pseudoeryx plicatilis</i> (L.) <i>Pseustes sulphureus</i> (Wagler) <i>Rhinobothryum lentiginosum</i> (Scopoli) |
| <ul style="list-style-type: none"> <i>Atractus torquatus</i> (D., B. & D.) <i>Chironius carinatus</i> (L.) ° <i>fuscus</i> (L.) <i>multiventris</i> Schmidt & Walker | <ul style="list-style-type: none"> + <i>Thamnodynastes strigilis</i> (Thunberg) ° <i>Xenodon severus</i> (L.) <i>Micrurus hemprichii</i> (Jan) <i>spixii</i> Wagler ° <i>surinamensis</i> (Cuvier) ° <i>Bothrops atrox</i> (L.) <i>bilineatus</i> (Wied) <i>brazili</i> Hoge ° <i>castelnaudi</i> D., B. & D. |
| <ul style="list-style-type: none"> ° <i>scurrulus</i> (Wagler) <i>Erythrolamprus aesculapii</i> (L.) <i>Helicops angulatus</i> (L.) + <i>leopardinus</i> (Schlegel) + <i>Hydrodynastes bicinctus</i> (Herrmann) ° <i>Hydrops triangularis</i> (Wagler) | <ul style="list-style-type: none"> + <i>Lygophis lineatus</i> (L.) ° <i>Oxybelis aeneus</i> (L.) <i>fulgidus</i> (Daudin) <i>Oxyrhopus petola</i> (L.) <i>Pseustes poeclionotus</i> (Günther) <i>Siphophis cervinus</i> (Laurenti) <i>Spilotes pullatus</i> (L.) ° <i>Tantilla melanocephala</i> (L.) <i>Tripanurgos compressus</i> (Daudin) <i>Xenodon rabdocephalus</i> (Wied) + <i>Crotalus durissus</i> (L.) <i>Lachesis muta</i> (L.) |

3 Widespread: 24 species, 17.9%.

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| <ul style="list-style-type: none"> ° <i>Boa constrictor</i> (L.) ° <i>Corallus enydris</i> (L.) ° <i>Epicrates cenchria</i> (L.) <i>Dipsas variegata</i> (D., B. & D.) <i>Chironius exoletus</i> (L.) ° <i>Clelia clelia</i> (Daudin) <i>Denärophidion dendrophis</i> (Schlegel) <i>Drymarchon corais</i> (H.Boie) <i>Imantodes cenchoa</i> (L.) ° <i>Leimadophis reginae</i> (L.) ° <i>Leptodeira annulata</i> (L.) ° <i>Leptophis ahaetulla</i> (L.) | <ul style="list-style-type: none"> + <i>Lygophis lineatus</i> (L.) ° <i>Oxybelis aeneus</i> (L.) <i>fulgidus</i> (Daudin) <i>Oxyrhopus petola</i> (L.) <i>Pseustes poeclionotus</i> (Günther) <i>Siphophis cervinus</i> (Laurenti) <i>Spilotes pullatus</i> (L.) ° <i>Tantilla melanocephala</i> (L.) <i>Tripanurgos compressus</i> (Daudin) <i>Xenodon rabdocephalus</i> (Wied) + <i>Crotalus durissus</i> (L.) <i>Lachesis muta</i> (L.) |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|



TABLE 2 (Continued 1)

4. Reaching eastern limit: 14 species, 10.4%.

<i>Leptotyphlops macrolepis</i> (Peters)	+ <i>Leimadophis melanotus</i> (Shaw)
<i>Typhlops minusquamis</i> Dixon & Hendricks	+ <i>Masticophis mentavarius</i> D., B. & D.
<i>Sibon nebulata</i> (L.)	+ <i>Mastigodryas pleei</i> (D., B. & D.)
<i>Atractus elaps</i> (Günther)	+ <i>Phimophis guianensis</i> (Troschel)
<i>major</i> Boulenger	+ <i>Pliocercus euryzonus</i> Cope
<i>Drymobius rhombifer</i> (Günther)	+ <i>Pseudoboa newwiedii</i> (D., B. & D.)
<i>Erythrolamprus bauperthuisii</i> D., B. & D.	+ <i>Micrurus isozonus</i> (Cope)

5. From Central or Northeastern Brazil: 12 species, 9%.

<i>Typhlops squamosus</i> (Schlegel)	<i>Liophis miliaris</i> (L.)
<i>Liotyphlops ternetzi</i> (Boulenger)	+ <i>Oxyrhopus trigeminus</i> D., B. & D.
<i>Leptotyphlops cupinensis</i> Bailey & Carvalho	+ <i>Phimophis guerini</i> (D., B. & D.)
+ <i>Cyclagras gigas</i> (D., B. & D.)	+ <i>Waglerophis merremii</i> (Wagler)
<i>Elapomorphus quinquelincatus</i> (Raddi)	<i>Xenodon newwiedii</i> (Günther)
<i>Leimadophis poccilogyrus</i> (Wied)	+ <i>Micrurus ibiboboca</i> (Merrem)



Fig. 6. Distribution of *Crotalus durissus* and *Lachesis muta* after Hoge (1965), Hoge & Hoge-Romano (1981) and Müller (1969).



1 A. Altitudinal endemic are those species with a distribution restricted to altitudes above 1000 m, usually inhabiting the summit or talus slopes of one or a few adjacent tepuis (sandstone tablemountains) (fig. 7). These snakes usually are only known from a few specimens and the distributions as plotted only reflect our scant knowledge of these creatures. As was recently demonstrated for *Bothrops lichenosus* Roze, which according to Da Cunha & Do Nascimento (1975) is a synonym of *B. castelnaudi* D., B. & D., they may turn out to be identical with widely distributed lowland species. At the moment we know of six species (4.5%) of snakes showing this distribution, all in southeastern Venezuela.

1 B. Lowland endemics are those species which occur below 1000 m and whose ranges do not (or only slightly) extend beyond the Guianan region (fig. 7). They may or may not occur to altitudes over 1000 m. Eventually part of the species considered to belong to this group may prove to have a much larger distribution. Among the 20 species (14.9%) this group, not less than 14 are burrowing snakes, which generally are difficult to collect (genera *Leptotyphlops*, *Apostolepis*, *Atractus*, *Leptomicrourus* and *Micrurus*).

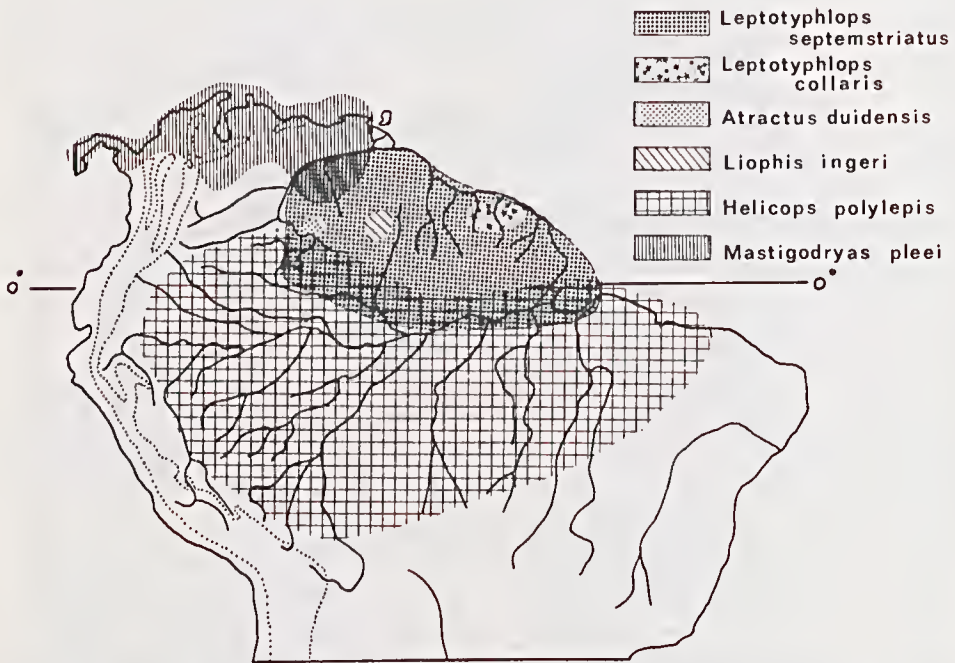


Fig. 7. Distribution of endemic species, of a species reaching Guiana from the northwest (*M. pleei*) and of a species with an Amazonian basin distribution (*H. polylepis*).



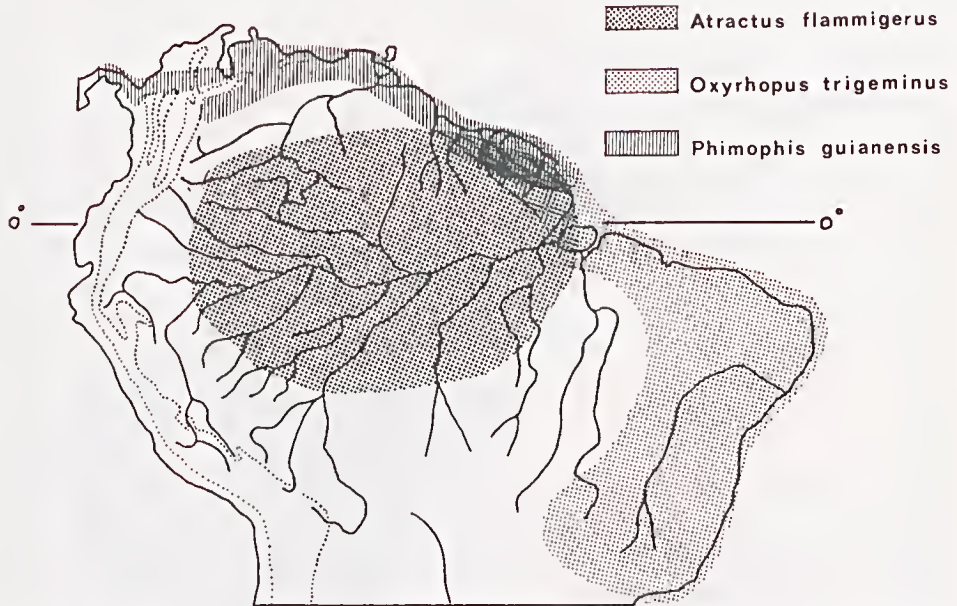


Fig. 8. Distribution of species with a wide range in Amazonia (*A. flammigerus*), reaching Guiana from central or northeastern Brazil (*O. trigeminus*) and reaching eastern limit in Guiana (*P. guianensis*).

Combining these data I come to a total of 26 species of endemic snakes, which ins 19.4% of the total number of snakes known to occur in Guiana.

2 A. Amazonian species with a periferal distribution along the northern and western edge of the Amazon basin (fig. 9). These species apparently are absent from central Amazonia, though their absence there is not easily explained. Hoogmoed (1979) pointed out that at least for one toad this distribution seems to be a result of its saxicolous way of life. For the 12 snakes (9%) showing this distribution pattern, the presence in Amazonia of close relatives or other ecological competitors may be the most important reason. I don't think that a distribution pattern with disjunct populations in upper Amazonia and Guiana, as e.g. postulated for *Ninia hudsoni* Parker by Duellman (1978), is real. So far, most of the species originally thought to show such a pattern have been found in the intermediate area as well.

2 B. Species of the Amazon basin, occurring on the southern edge of Guiana and along the eastern margin, where they may reach French Guiana (fig. 7). Only five species (3.8%) show this type of distribution, four of them (*Helicops hagmanni*, Roux *H. polylepis*, Günther *H. trivittatus* (Gray), *Hydrops martii* (Wagler) are watersnakes and are restricted to the immediate vicinity of the Rio Amazonas, whereas the fifth (*Rhadinea brevirostris* (Peters), not a watersnake) enters French Guiana and Surinam apparently from the east.



Fig. 9. Distribution of widespread species (*B. constrictor*), of peripheral Amazonian species (*D. anomalus*) and reaching Guiana from central Brazil (*C. gigas*).

2 C. Species widespread through Amazonia (fig. 8), often (22 out of 41) differentiated into several subspecies, make up the largest group, consisting of 41 species (30.6%). Generally these are forest-dwellers, a number of them are generalists which may also be found in edge and open situations and only five (*Helicops leopardinus* (Schlegel), *Hydrodynastes bicinctus* (Hermann), *Mastigodryas bifossatus* (Raddi), *Philodryas olfersii* (Lichtenstein), *Thamnodynastes strigilis* (Thunberg)) are restricted to open formations like savannas (two, *P. olfersii* and *M. bifossatus*) and swamps (the remaining three).

3. Widespread species ranging from Mexico or lower Central America over entire cis-Andean tropical South America (fig. 9). Usually (18 out of 24) these are differentiated into subspecies along various patterns. Only two *Lygophis lineatus* (L.) and *Crotalus durissus* (L.) out of 24 species are restricted to savanna habitat, the remainder are forest-dwellers or generalists. This group constitutes 17.9% of the total. It comprises both species with a Central American origin like the rattlesnake *C. durissus*, and species of South American provenance ranging into lower Central America, like *Corallus enydris* (L.).

TABLE 3

Comparison of rainforest snake-faunas in different regions in northern South America

FRF	Species in common				
	A	B	C	D	E
A. Western Guiana	85	70	60	60	44
B. Eastern Guiana	0.80	91	64	60	44
C. Bras. part Guiana	0.77	0.79	71	53	36
D. Iquitos	0.71	0.68	0.68	85	47
E. Santa Cecilia	0.64	0.61	0.58	0.68	53

TABLE 4

Comparison of snake-faunas characteristic for open formations in different regions in northern South America

FRF	Species in common				
	A	B	C	D	E
A. Western Guiana	20	13	10	2	0
B. Eastern Guiana	0.72	16	11	2	0
C. Bras. part Guiana	0.63	0.79	12	2	0
D. Iquitos	0.18	0.22	0.29	2	0
E. Santa Cecilia	0	0	0	0	0

TABLE 5

Comparison of open formation snake-faunas (including species restricted to this habitat and ubiquists) in different regions in northern South America

FRF	Species in common				
	A	B	C	D	E
A. Western Guiana	41	34	31	21	15
B. Eastern Guiana	0.87	37	32	21	15
C. Bras. part Guiana	0.84	0.91	33	21	15
D. Iquitos	0.65	0.69	0.74	24	17
E. Santa Cecilia	0.52	0.56	0.60	0.81	18



4. Species reaching their eastern distribution limit in Guiana may belong to different assemblages (fig. 7, 8). They may belong to species occurring in the upper Amazon basin (three), to species of northwestern South America (eight) or to species occurring in Central and northern South America (three). There is a relatively large proportion of savanna inhabitants (5 out of 14) and a low number polytypic species (three out of 14) in this group. Three of the savanna snakes (*Leimadophis melanotus* (Shaw), *Masticophis mentovarius* (D., B. & D.), *Mastigodryas pleei* (D., B. & D.)) just reach Guiana in its northwestern part, entering the savannas in the north of Estado Bolivar in Venezuela, which are connected with the extensive llanos of Central Venezuela and eastern Colombia; the other two (*Phimophis guianensis* (Troschel) and *Pseudoboa newwiedii* (D., B. & D.)) occur further east in the coastal savannas of the three Guianas. This group of 14 species constitutes 10.4% of the total.

5. The last group consists of species apparently reaching Guiana from northeastern, central or even southeastern Brazil (fig. 9). Among the 12 species (9%) of this group there is again a relatively large proportion of inhabitants of open formations. *Cyclagras gigas* (D., B. & D.) inhabits swampy areas, *Oxyrhopus trigeminus* D., B. & D., *Phimophis guerini* (D., B. & D.) and *Micrurus ibiboboca* (Merrem) inhabit dry, sandy savannas and may be considered as part of the cerrado-caatinga fauna of central and northeastern Brazil. Of several of the remaining species it is not clear to me which are their habitat preferences, but several more may turn out to be open formation snakes.

The wording employed in the description of several of the groups mentioned already indicates in which areas the species originated. For the endemics this is fairly uncomplicated, they apparently evolved within the confines of Guiana, either in a small isolated area, formed by a tepui, as is the case in the altitudinal endemics, or they evolved in lowland refugia in the Guianan region. As among the lowland endemics there are both forest and savanna species, two types of refugia are important here: savanna refugia and forest refugia. These refugia are thought to have been formed under the influence of changing climate in the Pleistocene and Holocene. Under wet climatic conditions savanna inhabitants were pushed back to relatively small, isolated patches of savanna, probably in the Roraima region on the border of Venezuela, Brazil and Guyana, and in the Paroe/Sipaliwini region on the border of Surinam and Brazil, whereas the forest inhabitants could spread widely through the area together with the expanding forests. During dry climatic conditions, the opposite happened: savanna inhabitants roamed far and lowland forest inhabitants were restricted to isolated patches of forest, probably the Guiana refuge on the northern versant of the Tumuc Humac Mountains in southern Surinam and French Guiana, and the Imeri and Imataca refuges in southeastern Venezuela (Haffer, 1979:140). These refuges are situated in areas where rainfall is high, compared with surrounding regions (figs. 1, 5). In the expanding phase of certain vegetations, after periods of isolation, when populations of one original species came in contact, they could either merge completely, with no reproductive barriers, behaving like one species; they could have differentiated enough to show ecological incompatibility, only merging in

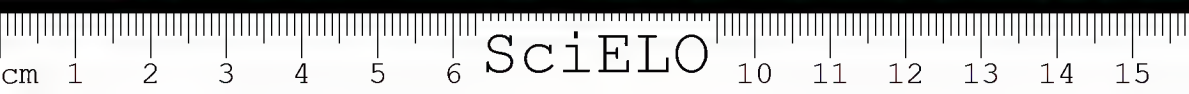
the zone of contact and for the greater part being allopatric, behaving like subspecies; or they could show complete reproductive isolation and behave like species, occurring sympatrically without any mixing of gene-pools. It will be evident that this process was not restricted to Guiana, but supposedly took place in all of South America, also influencing the evolution and distribution patterns of the other groups discerned here. In Amazonia several areas are recognised which could have served as refugia for vegetation and fauna with corresponding requirements and whence the entire Amazon basin could have been repopulated under favourable climatic conditions. However, distribution within this large area is not uniform and often different subspecies occur allopatrically. In the case of species with an Amazonian Arc distribution several closely allied species or ecologically similar species may be involved.

Sufficient distribution data and at least an indication of ecological requirements were available to permit comparison of snakefaunas from within Guiana with areas in the Amazon basin, viz., Iquitos (Dixon & Soini, 1977) and Santa Cecilia (Duellman, 1978). To this end the Guianan region was divided into three parts, e.g.: Western Guiana, the area west of the Essequibo River and Rio Branco; Eastern Guiana, Guyana east of the Essequibo River, Surinam, French Guiana and Amapa north of the Rio Araguari; and Brazilian Guiana, the area between Tumuc Humac Mountains and the Rio Amazonas. To get an impression of the amount of faunal relationship between these more or less natural subdivisions of Guiana mutually and with the outside localities mentioned, the Faunal Resemblance Factor (FRF) was computed for each combination of regions,

2C

using the formula: $FRF = \frac{2C}{N_1 + N_2}$ (Duellman, 1965, 1966) where N_1 and

N_2 are the numbers of species occurring in any two regions and C is the number of species common to the two regions compared. In tables 3-5 the total number of species in each locality is on the diagonal (bold face lettering) from upper left to lower right. The number of species common to each combination of regions is to the right and above the diagonal with the totals. To the left and below the diagonal are the Faunal Resemblance Factors. Comparison of the FRF's for the three Guianan region shows that there is a great resemblance between those regions, without indication of a break somewhere. For forestsnakes there is a fairly good resemblance with both Iquitos and Santa Cecilia, but in all cases this resemblance is slightly greater for Iquitos than for Santa Cecilia, which is farther removed from the Guianan region. The data suggest a gradual transition along an east-west gradient, both within Guiana and from Santa Cecilia to Iquitos to Guiana. However, sufficient data from the area between Iquitos and Guiana are lacking and also, considering the list of snakes recorded for Santa Cecilia I get the impression that it is less complete than that of Iquitos. This impression is reinforced by the FRF between Iquitos and Santa Cecilia for rainforest snakes, 0.68, which is much less than might be expected for areas not separated by barriers. Nevertheless, it seems to make sense to postulate that the rainforest snakes are fairly evenly distributed throughout Amazonia and Guiana, differences being caused by species with relatively small distribution



areas in respectively upper Amazonia and lowland Guiana. For snakes restricted to open formations there also is good resemblance between the several areas within Guiana, but there is only a slight resemblance with the Iquitos region and none at all with Santa Cecilia where no open formations and species associated with them, occur (Duellman, 1978). When considering all snakes which may be found in open situations, the picture is different. There is a fair resemblance between Iquitos and the Guianan regions, and only a moderate one between Santa Cecilia and the Guianan regions.

From the FRF's no distinct break between the compared rainforest snakefaunas is evident and it is only possible to conclude that for these snakes there are no unsurmountable barriers between the Andes and the mouth of the Rio Amazonas. Within Guiana rainforest snakes are evenly distributed. The Essequibo River does not constitute a barrier for them as it does e.g. for frogs (Hoogmoed, 1979). For savanna snakes the picture is slightly different. Here we find a high resemblance between the Brazilian part of Guiana and eastern Guiana, whereas the resemblance of each of these parts with western Guiana is distinctly lower. Upon closer examination it appears that this difference within Guiana is not due to the presence of any barrier, but can be explained on the one hand by the presence in western Guiana of a few snakes which just cross the Orinoco and enter Guiana from the llanos, and on the other hand by the presence in eastern Guiana and the Brazilian part of Guiana of species reaching those areas from central or northeastern Brazil and not (yet) penetrating beyond Surinam.

CONCLUSIONS

The snakefauna of the Guianan region as we know it today is a composite of species of different origins. The largest fraction consists of Amazonian species, of which the ones with a wide range in Amazonia form the majority. These probably originated in the Napo lowland rainforest refuge at the eastern base of the Andes in Ecuador/Peru, whence they dispersed eastward after the onset of wetter climatic conditions. The group with an Amazonian basin distribution probably evolved in galleryforests along the Rio Amazonas, whereas the distribution of snakes having a periferal distribution might be explained by their having differentiated in submontane forest refuges along the eastern flank of the Andes. Species with a distribution encompassing both Central and South America may have originated either in Central or in South America, from where they expanded into the adjacent region. The majority is of South American provenance, only five (*Imantodes cenchoa* (L.), *Leptodeira annulata* (L.), *Leptophis ahaetulla* (L.), *Tantilla melanocephala* (L.) and *Crotalus durissus* (L.)) invaded South America from Central America. These species either evolved in savanna refugia (*C. durissus* (L.), *Lygophis lineatus* (L.)), or they evolved in forest refugia. The majority of the forest species has a wide range in South America and evolved into subspecies which may be indicative for the refuges in which the species survived (well demonstrated by for instance

the distribution of *Lachesis muta* (L.) (fig. 6). Species which only occur in western Guiana mostly are invaders from the west (NW South America, Central America) or from the southwest (Upper Amazonian basin), but *Pseudoboa newwiedii* (D., B. & D.) may be a former endemic of Guiana that extended its range to the northwest, to reach Panama. Species occurring in eastern Guiana, not reaching further west than Surinam, apparently are invaders from the southeast. The savanna inhabiting species in this group evolved in savanna refugia in northeastern and central Brazil. They probably reached Guiana via a wide belt of cerrado-like vegetation, connecting northeastern Brazil with southeastern Venezuela, during the last arid period (figs. 4, 5). When the climate became more humid and the forests expanded again, these species were left stranded on the isolated savannas of Guiana, most of them in the east. The rainforest species in this group probably evolved in a rainforest refuge south of Belém.

The lowland endemics mainly are forestsnakes and for them possible refuges in Guiana are important: Guiana —, Imataca — and Imerí refuges. Of the altitudinal endemics at least four are savanna species and they may have evolved in the open formations covering the tops of certain Venezuelan tepuis. For the other two altitudinal endemics (*Atractus duidensis* Roze, *Liophis trebbawi* Roze) habitat data are not available.

Endemism in Guianan snakes is not particularly high (19.4%) compared to that in amphibians (52%) or reptiles in general (27%), but still is considerable. Part of this level of endemism undoubtedly is due to our poor understanding of many South American snake genera, notably *Atractus*, *Oxyrhopus*, *Leptotyphlops*, and the scarcity of certain species in collections. Future research should continue assembling distribution data, which are still badly needed for many species from many areas, and one of the main objectives should be to gather basic ecological data, to establish niche preferences, food consumed, reproductive strategy, etc. When this information becomes available, zoogeographic analysis of South American snakes can be more fruitful and more firmly based than hitherto.

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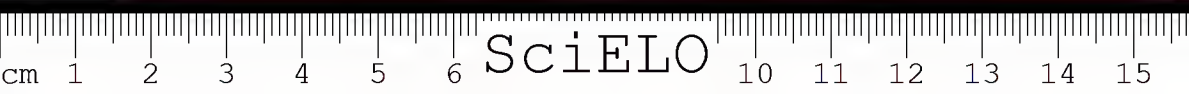
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APPENDIX I

Species reported from Guiana

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
	authors																													
<i>Liotyphlops temerizi</i> (Boulenger)																					S	S	G		S	S	G			
<i>Typlophlops squamosus</i> (Schlegel)																					GBr				S	S	G			
<i>Lepotyphlops amazonica</i> Orejas-Miranda collaris Hoogmoed																					GBr				GBr	V	V	G	G	C
<i>Cypripetia</i> Bailey & Carvalho <i>dimidiatus</i> (Jan)																										Br	G	G	V	C
<i>macrotis</i> (Peters) <i>sepienfructus</i> (Schneider)																						S				G	G	G	V	C
<i>tenella</i> Klauber <i>Typlophlops brougermones</i> Vanzolini <i>lumbriciata</i> (L.) <i>mansuetor</i> Dixon & Hendricks <i>reticulata</i> (L.) <i>Antia</i> s. <i>eydala</i> (L.)		S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	G	SC	BC				(B)	(S)		(G)	(G)			X
<i>phaliporum</i> Roze <i>Boa c. constrictor</i> L. <i>Corallus caninus</i> (L.) <i>e. erydora</i> (L.) <i>cockii</i> Gray		S		S	S			S					S	S	S	S	B	G	B	G	Br	S			V	V	V	V	V	V
<i>Epiplatys e. erckbia</i> (L.) <i>mouras</i> Gray <i>Ewaectes decahisporae</i> Dunn & Conant <i>m. murinus</i> (L.)							S	S	S			S	S	S	S	S	B	C	BC		S	BC	S	A	V	G	G			X
<i>gigas</i> (Latreille) <i>Dipsosa caelestis</i> (Scribner) <i>copri</i> (Günther) <i>i. indica</i> Laurenti <i>patavinus</i> Schlegel <i>v. variegata</i> (D., B. & D.) <i>Sibon n. nebulosa</i> (L.) <i>Apostolepis quinquefasciata</i> Boulenger <i>Atractus bohai</i> (Boie) <i>daudreana</i> Roze <i>elaps</i> (Günther) <i>fonae</i> (Filippi) <i>flammigerus</i> (Boie) <i>inaspida</i> Roze <i>latifrons</i> (Günther) <i>Atractus major</i> Boulenger <i>rivieroi</i> Roze <i>schacki</i> (Boie) <i>steyermarki</i> Roze <i>torquatus</i> (D., B. & D.) <i>trilineatus</i> Wagler <i>zidiki</i> Giac & Rodrigues		S										SC				S	B	SC	B	S	BSBr	C	S	BSBr	S	S	S	S	S	S
<i>Cerropia aurata</i> (Schlegel) <i>Chironius c. carinatus</i> (L.) <i>exoleius</i> (L.) <i>f. fuscus</i> (L.) <i>m. multiventris</i> Schmidt & Walker <i>cochranus</i> Hoeg & Romano <i>coraularis</i> (Wagler)																														
<i>Clelia c. cilia</i> (Daudin) <i>Cyclograpsus gigas</i> (D., B. & D.)																														

APPENDIX 1 (continuation)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
Species reported from Guiana in error																														
<i>Cylindrophis maculatus</i> (L.) <i>rufus</i> (Laur.)		S	S	S	S	S	S	S	S	S	S	S																		
<i>Epicratis ocellifer</i> Bibron																														
<i>Akodon erythrogrammus</i> (Daudin)																														
<i>Akserulla prasina</i> (Bois)																														
<i>Dipsos inermis</i> (Jan)																														
<i>Helicops cornuta</i> (Wied)																														
<i>Heliconia</i> <i>infracturatus</i> (Jan)																														
<i>Homalopsis buccata</i> (L.)																														
<i>Lampropeltis triangulum</i> (Lacépède)																														
<i>Leopoldia carsoni</i> (Lacépède)																														
<i>Leopoldia</i> <i>triacis</i> (L.)																														
<i>Maniophis melanoleucus alternatus</i> (Bocourt)																														
<i>Natrix natrix</i> (L.)																														
<i>Oxyrhynchus petola</i> <i>arbae</i> D., B. & D.																														
<i>Philodryas s. elegans</i> (Tchudi)																														
<i>Sibynomorphus mikonisii</i> (Schlegel)																														
<i>Siphlophis pulcher</i> (Raddi)																														
<i>Aspidoleps habitus</i> (Laur.)																														
<i>Micruurus tovarillanus</i> (Merrem)																														
<i>Helicopsis</i> <i>fulviventris</i> (Günther)																														
<i>longirostris ornata</i> (Jan)																														
<i>Vipera berus</i> (L.)																														
" <i>Aspis latitonda</i> L."																														
" <i>Plataspis laurentii</i> Daud."																														
<i>Typophis unicoloratus</i> (D. & B.)																														
<i>Okhovius bicarinatus</i> (Wied)																														
Total species in error		2	—	5	1	1	1	—	3	2	4	1	—	—	1	5	4	5	—	5	—	3	1	4	2	—	3			

Legend of Appendix 1.

Guianan snakes, check list and growth of knowledge about this group (also cf. fig. 3). 1 = Warren (1867), 2 = Merian (1705a,b), 3 = Seba (1734-35), 4 = Scheuchzer (1735a,b; 1738), 5 = Sundius (1749), 6 = Gronovius (1756), 7 = Linnaeus (1758), 8 = Houtvyn (1764), 9 = Linnaeus (1766), 10 = Laurenti (1768), 11 = Linck (1783), 12 = Gmelin (1789), 13 = Daudin (1803 a-d), 14 = Fitzinger (1826), 15 = Schlegel (1826), 16 = Tröschel (1843), 17 = Duméril, Bibron & Duméril (1844-54), 18 = Gray (1849) + Günther (1858), 19 = Jan. & Sordani (1860-81), 20 = Kappeler (1885), 21 = Eonlenger (1893-96), 22 = Van Lidth de Jeude (1898, 1904, 1914/17), 23 = Amaral (1930), 24 = Roze (1966), 25 = Peters & Oréjas-Miranda (1970), 26 = Hoogmoed (1979), 27 = Lancini (1979), 28 = Casac & Rodriguez (1980b), 29 = present paper. A = Northern South America, Am = Amazonian basin, B = (British) Guyana, Br = Brasil, C = French Guiana, G = Guiana, S = Surinam, V = Venezuelan Guayana, X = taxa recorded from Guiana since 1979 or overlooked till now, Letters between brackets indicate introduced species.

PROBLEMS AND APPROACHES IN THE INTERPRETATION OF THE EVOLUTIONARY HISTORY OF VENOMOUS SNAKES

John E. CADLE *

ABSTRACT: Data from the literature bearing on the phylogenetic relationships among higher taxa of advanced snakes are reviewed in an attempt to resolve the question of how many parallel evolutionary events have resulted in front-fanged venom delivery systems. Two specific events, that of the New World coral snakes (Micrurines) and the African mole viper (*Atractaspis*), are discussed in detail, and molecular evidence comprising immunological comparisons of serum albumins are brought to bear on the relationships of these taxa. The molecular evidence do not support the hypothesized affinity of either of these groups to colubrids, and strongly support the relationship of micrurines to the elapids. *Atractaspis* is not unambiguously allied with either viperids or elapids by molecular criteria, and may represent a lineage independent of these and of the colubrids. It is concluded that there are reliable data upon which to suggest the parallel evolution of front-fanged venom delivery systems in at most three lineages: *Atractaspis*, viperids, and elapids. Hypotheses suggesting the evolution of these systems from within colubrids are discounted.

Problems with the current data base and approaches to the phylogeny of advanced snakes are highlighted, and suggestions for formulating and testing additional hypotheses are made. Front-fanged venom delivery systems in advanced snakes may have evolved fewer times than some current theories suggest, but more robust phylogenetic hypotheses are necessary to formulate specific tests.

INTRODUCTION

The adaptive radiation of advanced snakes (Caenophidia or Colubroidea) has produced a diverse array of species that inhabit most of the world's terrestrial habitats, as well as some aquatic and marine forms. They are traditionally divided into three families, the Colubridae containing about 80% of the species, and two front-fanged venomous groups, Elapidae and Viperidae, with less extensive radiations. Numerous problems exist with attempts to reconstruct the evolutionary relationships

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and history of these groups. The paucity of fossil material combined with extensive parallelism in morphological features (Rabb and Marx, 1973; Underwood, 1967) has prevented the formulation of robust phylogenetic hypotheses, resulting in considerable instability of higher taxonomic categories.

One of the pervasive morphological themes among the advanced snakes is the evolution of venom delivery systems (Underwood, 1967; Rabb and Marx, 1973). Though some members of the Colubridae show no dentitional or other specializations associated with venom delivery, many species have enlarged rear teeth associated with specialized venom-secreting (Duvernoy's) glands, and species of two genera (*Dispholidus* and *Thelotornis*) are known to be highly venomous. The front-fanged venomous snakes exhibit two structurally different types of venom apparatus. Proteroglyph dentition, consisting of hollow fangs on relatively elongate and non-rotatable maxillary bones, is found in all elapids. In viperids, on the other hand, the fang-bearing maxillary bone is extremely short and rotatable so that the fangs can be erected (solenoglyph dentition). In addition, the elapids and vipers differ in other aspects of the morphology of the venom apparatus (muscles, glands) and they differ generally with respect to the biochemical nature of the components of the venom itself (Kochva, 1979; Lee, 1979).

Much of the taxonomic instability of the advanced snakes centers on the questions of how many times particular venom delivery systems have evolved (see Bougeois, 1965; McDowell, 1968; and Savitzky, 1978 for discussions). A critical question has been whether or not the front-fanged venomous snakes (Viperidae and Elapidae, omitting for the present the problematic genera *Homoroselaps*, *Atractaspis*, and *Micrurus*) stemmed from a common ancestor with front fangs, or whether they represent independent derivations of specialized venom delivery systems. Boulenger (1893) proposed that vipers and elapids had independent origins among the colubrid snakes, and subsequent work on jaw musculature (Haas, 1938, 1952, 1962), trunk musculature (Mosauer, 1935), and the venom gland and its musculature (Kochva, 1962, 1963, 1978) reinforced this view. Other workers (Mahendra, 1938; Bogert, 1943; Johnson, 1955, 1956; Dowling, 1959; Marx and Rabb, 1965; Klauber, 1972; Rabb and Marx, 1973) adhered to the view advocated by Cope (1900) that the viperids and elapids were more closely related to each other than either was to the colubrids. This particular problem is a reflection of a more general problem encountered in attempts to unravel phylogeny among advanced snakes: How are the parallelisms, to be recognized?

Recent discussions of the evolution of venom delivery systems in snakes have increasingly invoked parallelism to explain the attainment of front-fanged conditions (proteroglyphy or solenoglyphy) in presumably unrelated taxa of advanced snakes. Currently, there are five such postulated parallel events described in the literature: Viperidae, Elapidae, *Atractaspis*, *Homoroselaps*, and New World coral snakes. Fouin (1969) suggested a sixth parallel attainment of a front-fanged venom delivery system in the elapid genus *Elapsoidea*, but this work has been reinterpreted

by Savitzky (1978) as not supporting such a hypothesis and it will not be considered further here.

Tests of hypotheses of parallelism must begin with an hypothesis of the evolutionary relationships among the taxa involved, for parallelism is evidenced by the appearance of identical derived character states in nonsister taxa. Thus, characters evolved in parallel will be discordant with a phylogeny based on characters which accurately reflect the evolutionary history of a particular group. For analyses of parallelism, the reference phylogeny should be supported using as many character sets as possible. Morphological data are commonly used to construct these phylogenetic hypotheses, though any data which can be analyzed phylogenetically can provide useful information. Recently, molecular data have made significant contributions in this regard (see for examples, Cronin and Meikle, 1979; Sarich and Cronin, 1976; Larson *et al.*, 1980). These data are especially useful as an independent assessment of relationships based on morphological criteria, and can be used alone or in conjunction with morphological data to corroborate or refute specific phylogenetic hypotheses. Because molecular evolution can be shown to be a largely divergent process (Wilson *et al.*, 1977), it can be extremely valuable in allowing the detection of parallelism in morphology. Recent applications of molecular data to evaluate suggested cases of parallelism have corroborated the monophyly of the ratite birds Prager *et al.*, 1976) and of the hystricognath rodents (Sarich and Cronin, 1980), and have shown the association of the catarrhine and platyrrhine primates (Sarich and Cronin, 1976, 1980), of the giant panda with the bears (Sarich, 1973), of *Cynocephalus* (Dermoptera) with the primates (Cronin and Sarich, 1975), and of the New World coral snakes with other elapids (Cadle and Sarich, 1981). In each of these cases, the hypothesis of parallelism in the morphology of the taxa concerned has been refuted.

A detailed analysis of the relationships among suprageneric taxa of advanced snakes from the standpoint of molecular data requires data from a broader array of taxa than are presently available, and will be the subject of future reports. Here I restrict my discussion to two examples which have figured prominently in discussions concerning the parallel acquisition of front-fanged venom delivery systems in snakes, and which illustrate my approach in the application of molecular data to problems in snake systematics. I will then highlight some of the problems encountered in attempts to analyze the evolution of snake venom delivery systems, and put these into a more general perspective relative to the phenomenon of parallelism and the phylogeny of such complex adaptations.

The approach used involves immunological comparisons of serum albumins with the microcomplement fixation assay, a procedure described in detail by Champion *et al.*, (1974). This method basically detects sequence resemblance between homologous proteins in different species by using antisera to proteins from reference species. The data I will discuss are expressed in albumin immunological distance units (AID units), which may be subjected to a variety of numerical techniques to construct hypotheses of phylogenetic relationships. For further discussion of these approaches see Champion *et al.* (1974), Sarich and Cronin (1976), and Prager and Wilson (1978).



The two examples I discuss are the New World coral snakes (Savitzky, 1978) and the African mole viper *Atractaspis* (Bourgeois, 1965). Both of these groups are front-fanged venomous snakes (proteroglyphous and solenoglyphous respectively) and were seen as derived from specific colubrid lineages. According to these phylogenetic hypotheses their venom delivery systems would be derived in parallel with those of true elapids and vipers.

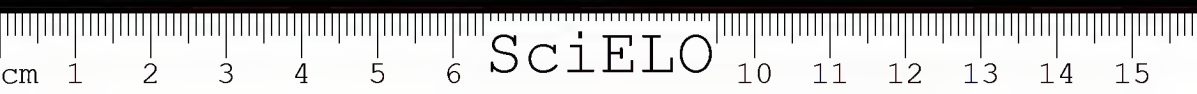
The immunological data bearing on the relationships of the micrurines have been extensively discussed elsewhere (Cadle and Sarich, 1981), and will only be briefly reviewed here. Immunological data bearing on the second case, *Atractaspis*, are as yet incomplete, but the data now available are at variance with some interpretations of the relationships of this genus, and they suggest areas where more work is needed to resolve the phylogenetic affinities of this enigmatic snake. A more detailed consideration of the molecular data for *Atractaspis* will form a separate report.

THE NEW WORLD CORAL SNAKES (MICRURINES)

New World coral snakes (*Micruroides* and *Micrurus*) are a speciose (approximately 50 species) but morphologically a rather conservative group distributed from the southern United States to Central Argentina. Traditionally coral snakes have been considered the sole New World representatives of the family Elapidae (McDowell, 1967, 1969). However, Savitzky (1978) suggested that these snakes were derived *in situ* in the neotropics from snakes allied to *Apostolepis* and *Elapomorphus* ("elapomorphines"), part of a very extensive New World colubrid radiation, the xenodontines.

Apostolepis and *Elapomorphus* are widely distributed throughout much of South America east of the Andes, but especially in southeastern Brazil and the surrounding region. They exhibit a number of features associated with fossoriality, including fusion of head scales, robust nasal complex, reduced tooth number, depressed vertebrae, and short quadrates, and many of these features are also found in micrurines (Savitzky, 1978). Savitzky suggested that for many morphological characteristics with the exception of the venom delivery system, the morphological character states of extant elapomorphines could be arrayed in a smooth morphocline with those of micrurines, and he used this to argue for a close relationship between the two groups. Savitzky regarded similarities in the venom delivery system between micrurines and Old World elapids as parallel attainments, and suggested that such adaptive features would likely arise in parallel.

Cadle and Sarich (1981) compared serum albumins from representative elapids, micrurines, and xenodontines by microcomplement fixation. Using antisera to xenodontine species the average immunological distance to species of micrurines are very similar to those measured to Old World elapid species (Table 1), indicating no particular xenodontine-micrurine affinities. *Micrurus* albumin is more similar to those of the



Old World elapids than of xenodontines [the similar average distances to xenodontine species using either Anti-*Micrurus* or Anti-xenodontine sera partly reflects the conservative nature of the elapid albumins (Cadle and Sarich, 1981) and partly the observation that xenodontines are not a natural phylogenetic grouping (Cadle, in prep.)]. Cadle and Sarich lacked a sample of an elapomorphine species for biochemical analysis. Their conclusions, however, were justified since there is little question that this group comprises part of the xenodontine radiation, several species of which were included in their study. An analysis of albumin immunological data on seven genera of advanced snakes (Cadle and Sarich, 1981, Table 1) resulted in the phylogenetic hypothesis reproduced here as Fig. 1. *Micrurus* associates unambiguously with *Laticauda*, an elapid suggested by MacDowell (1967, 1969) to be among the closest living relatives of the micrurines. These data were used by Cadle and Sarich (1981) to advocate the retention of the micrurines within the family Elapidae.

TABLE 1

Average albumin immunological distances among xenodontines, micrurines, and Old World elapids. Data are from Cadle and Sarich (1981) and Cadle and Gorman (1981)

Antisera

	Xenodontines			Micrurines	Old World Elapids	
	<i>Clelia</i>	<i>Leptodeira</i>	<i>Coniophanes</i>	<i>M. spixi</i>	<i>Laticauda</i>	<i>Hydrophis</i>
Micrurines	91	110	94	—	48	—
Old World Terrestrial Elapids	83	106	86	47	28	28
Sea Snakes	91	96	77	50	—	—
Xenodontines	87	78	81	87	72	—

Since the Cadle and Sarich study I have compared the albumin of *Micrurus* with a suite of other xenodontine genera using microcomplex fixation, and the unequivocal separation of micrurines from this group is maintained. In addition, I recently acquired a blood sample of an elapomorphine, *Apostolepis assimilis*. Comparisons of this species to two xenodontine albumin antisera, Anti-*Philodryas viridissimus* and Anti-*Clelia scytalina*, gave immunological distances of 40 and 38, respectively, while using Anti-*Micrurus spixi* the comparable immunological distance was 82. This latter value is again typical of the measured immunological distances between *Micrurus* and xenodontines (Table 1; Cadle and Sarich, 1981), while the AID's to the two xenodontine species strongly suggest that *Apostolepis* is a part of this radiation. No association between *Apostolepis* and micrurines is indicated by these data.



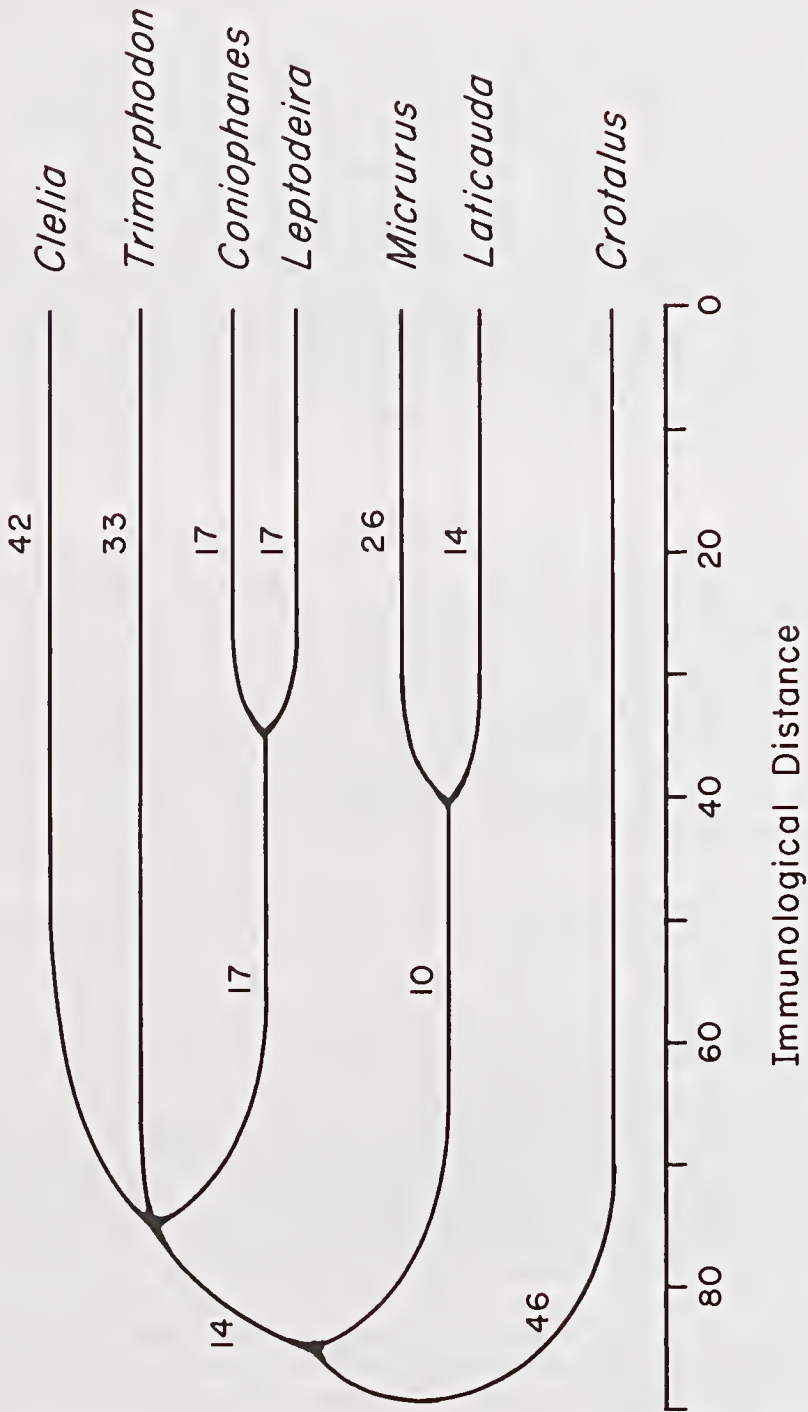


Fig. 1. An hypothesis of the phylogenetic relationships among seven genera of advanced snakes derived from the data of Table 1 in Cadle and Sarich (1981) using the algorithm of Sarich and Cronin (1976).



The available molecular data are clear on the association of coral snakes with other elapids, and alternative interpretations of the morphology of micrurines relative to other elapids are also consistent with this view (McDowell, 1967, 1969; C. J. McCarthy, pers. comm.). Cadle and Sarich (1981) argued that the morphological differences between micrurines and other elapids documented by Savitzky (1978) reflected the long period during which the New World lineage had been separated from the Old World lineages of the family. The most parsimonious interpretation of all comparative evidence, then, would appear to be a phylogenetic grouping uniting micrurines with Old World elapids, and substantially differentiated morphologically and biochemically from neotropical colubrids. Under this interpretation, the hypothesis of parallelism in the evolution of a front-fanged venom delivery system in micrurines is falsified.

ATRACTASPIS

Atractaspis, the African mole viper, has long been considered a viperid though recognizably a very distinctive one (Haas, 1962; Kochva, 1962; Laurent, 1950). Bourgeois' (1965) radical hypothesis that the genus is related to aparallactine colubrids generated much research on their morphology and on the composition of their venom (see McDowell, 1968; Kochva and Wollberg, 1970; Kochva et al., 1967; Parnas and Russell, 1967; Underwood, 1967; Minton, 1968). The Aparallactinae was erected by Bourgeois to include *Atractaspis* and a variety of small colubrid genera, many of which are highly modified for a fossorial existence. Currently, about twelve genera are assigned to this group (Savitzky, 1978) and its species are widely distributed in Africa (*Atractaspis* also occurs in the Middle East). The group has been characterized by both Bourgeois (1965) and McDowell (1968). Bourgeois attached special significance to a presumed morphocline in the nature of the prefrontal-maxillary articulation in aparallactines which culminates in the unique fang erecting mechanism of *Atractaspis*. This feature appears quite variable within the aparallactines (judging from Bourgeois' figures) and was not used by McDowell to diagnose the group.

No consensus on the relationships of *Atractaspis* prevails, with some workers adhering to Bourgeois' hypothesis of aparallactine affinities (McDowell, 1968; Liem et al., 1971; Parker and Grandison, 1977; Savitzky, 1978), and with others suggesting that the evidence, particularly from the structure of the venom apparatus and head muscles lends only weak support to such an association (Kochva et al., 1967; Kochva and Wollberg, 1970; Heymans, 1975). Certain aspects of head structure and venom composition suggested elapid affinities (Kochva et al., 1967; Parnas and Russell, 1967; Minton, 1968; Kochva and Wollberg, 1970), but the structure of the venom apparatus itself conforms to neither the viperid nor the elapid patterns (Kochva 1978). Thus, there seems to be a consensus on only one point: *Atractaspis* differs markedly from "typical" vipers in many aspects of morphology and venom chemistry (see references cited above).

The comparative albumin immunological data which I have had available at this time are too incomplete to resolve the question of how *Atractaspis* fits relative to other major lineages of advanced snakes, though it is quite distinct from all genera to which comparisons have been made thus far. The data which are available (Table 2) suggest that further studies, molecular and morphological, are necessary before definitive conclusions can be drawn. I have had available for biochemical studies only four species representing two genera of aparallactines (*Aparallactus* and *Amblyodipsas*; Table 2), and I have produced antisera to albumins of *Atractaspis bibroni* and *Amblyodipsas polylepis*. Using Anti-*Atractaspis* albumin, no association of this genus with the four available aparallactine species is apparent (average of 96 AID units), nor is there an association with the two viperids included (average 96 AID units). The average of reciprocal immunological distance measurements between *Atractaspis bibroni* and *Amblyodipsas polylepis* (90 AID units) is of the same order. All of these AID values are typical of those found between major groups of advanced snakes (family level), where one generally finds 75-100 units of change between taxa (Cadle, unpublished).

TABLE 2
Albumin immunological distances among *Atractaspis*, Viperids, Elapids, and Aparallactine colubrids

	Anti- <i>Atractaspis</i> <i>bibroni</i>	Anti- <i>Amblyodipsas</i> <i>polylepis</i>
<i>Atractaspis bibroni</i>	0	87
Viperids		
<i>Crotalus enyo</i>	93 (80)*	—
<i>Bothrops atrox</i>	98 (90)	—
Elapids		
<i>Micrurus spixi</i>	74	—
<i>Laticauda scmifasciata</i>	72	—
<i>Hydrophis melanosoma</i>	71	—
Aparallactine colubrids		
<i>Aparallactus capensis</i>	104	91
<i>Aparallactus concolor</i>	105	90
<i>Amblyodipsas polylepis</i>	93	0
<i>Amblyodipsas unicolor</i>	83	18

* Values in parentheses are reciprocal immunological distances corrected for non-reciprocity (Sarich and Cronin, 1976) and averaged.

Clearly, these results cannot be taken as a definitive statement on the relationships of *Atractaspis*. In particular, the molecular data on intra-viperid and intra-elapid relationships need to be expanded beyond those currently available. Within the viperids, of all comparisons made thus far, the genus *Causus* is the furthest removed from *Crotalus* (AID's of 64 and 66 to *C. resimus* and *C. maculatus*, respectively);

similarly, intra-elapid AID's do not approach the elapid-*Atractaspis* distances when reciprocity and rates of change considerations are met. Thus, while the *Atractaspis*-elapid AID's reported in Table 2 are lower than those to viperids or aparallactines, using two anti-elapid sera, the AID's to *Atractaspis bibroni* are much higher: 89 (using Anti-*Dendroaspis polyepis*) and 87 (using Anti-*Elapsoidea semiannulata*). Hence, the currently available molecular data do not indicate an affinity between *Atractaspis* and either elapids or viperids, and they strongly suggest that the inclusion of *Atractaspis* among the aparallactine (or other) colubrids is premature, a conclusion also reached by Kochva and Wollberg (1970) on the basis of venom gland structure and histology.

The immunological data further suggest that additional studies of the relationships of aparallactines are warranted. The AID's between *Amblyodipsas* and the two species of *Aparallactus* (Table 2) are as great as those between either of these genera and *Atractaspis*. Molecular data on additional aparallactine genera would clearly be desirable. Certain morphological comparisons in addition to those already mentioned suggest that the aparallactines as currently recognized are a quite variable group. Heymans (1975) reported differences in the arrangement of mandibular muscles both within aparallactines (*Chilorhinophis* and *Aparallactus* compared) and between *Atractaspis* and either of these. In addition, Kochva and Wollberg (1970) reported considerable variability in the structure of aparallactine oral glands; in particular, they found the glands of *Amblyodipsas* (*Calamclaps*) differed considerably from those of *Aparallactus*, and imply that these genera may belong to different colubrid lineages, an interpretation consistent with the limited immunological comparisons reported here. Conclusions concerning the phylogenetic unity of the Aparallactinae are difficult to assess from such comparisons, however. A more comprehensive study of aparallactine genera and the inclusion of outgroups would be required to draw firm phylogenetic conclusions from these data. An assessment of how these features vary within other welldefined colubrid groups would also enhance their value in this particular case.

To summarize, the distinctiveness of *Atractaspis* relative of other vipers and to colubrids is the only consistent result obtained using all available sources of data, and this hypothesis can be considered corroborated (sensu Nelson, 1979; Nelson and Platnick, 1981). Hypotheses suggesting affinity to aparallactines (Bourgeois, 1965; McDowell, 1968) are not corroborated by further morphological (Kochva *et al.*, 1967; Kochva and Wollberg, 1970; Heymans, 1975) or molecular (this paper) data. Thus *Atractaspis* may represent an independent lineage of front-fanged snakes; its close relatives, if any exist, are as yet undetected.

FRONT FANGED VENOM DELIVERY SYSTEMS AND THE COLUBRIDAE

Kochva and Wollberg (1970) urged caution in changing the taxonomic status of venomous snakes because of their medical importance. Such caution is also in the interest of workers attempting to understand the



phylogeny and evolution of the biochemical and morphological components of the venom delivery system. The currently available molecular data on the relationships of two venomous taxa of advanced snakes, the micrurines and *Atractaspis*, do not support their hypothesized close relationships to specific colubrid groups (xenodontines and aparallactines, respectively). A consideration of the other comparative evidence certainly does not require such associations, and, indeed, in at least the case of the micrurines, can be more parsimoniously interpreted in alternative ways. Kochva and Wollberg further suggested that the morphological data of Bourgeois (1965) and of McDowell (1968) were insufficient to ally either *Atractaspis* or *Homoroselaps* with the aparallactines, a conclusion with which I agree. These results call for a reconsideration of the question posed at the beginning of this paper: How many times have front-fanged venom delivery systems evolved independently among advanced snakes?

I conclude that no undisputed evidence exists for the evolution of front-fanged venom delivery systems from within any lineages of living colubrids. Kochva and Wollberg (1970) and Cadle and Sarich (1981) argue for retention of *Homoroselaps* and the micrurines, respectively, in the Elapidae. The case of *Atractaspis* presents special problems since unambiguous evidence of any sort associating this genus with any other taxon does not exist at the present time, but there is no compelling evidence associating even this genus with the Colubridae as has been proposed, and the molecular data in particular preclude such an association. Thus, the available evidence indicate that only three possibilities exist for the parallel evolution of front-fanged venom delivery systems: the solenoglyph systems of viperids and *Atractaspis*, and the proteroglyph system of elapids (*sensu lato*). I do not feel that a decisive resolution of the problem is possible given present data, and there are certain problems with current approaches to the question. I will attempt to highlight these in the next section, and suggest ways that we might profitably approach a solution to the other questions already posed.

PARALLELISM AND THE EVOLUTION OF VENOM DELIVERY SYSTEMS

Parallelism among lineages is usually inferred for one of three reasons. The most commonly cited evidence, and the most robust, is that different character sets produce discordant phylogenies. This has been used, for example, to demonstrate the parallel evolution of foot morphology among geckos (Russell, 1979). Second, parallelism has occasionally been inferred between two groups because of their widely disjunct geographical distributions, accompanied by plausible fossil ancestral groups in the areas occupied by living forms (suggested, but not corroborated, for New and Old World monkeys). Finally the extreme specialization of some organisms have obscured true phylogenetic affinity between related forms and led to the suggestion of parallelism (e.g., the suggested parallelism between the giant panda and bears). Of all of these means of inferring parallelism, the first is clearly to be preferred

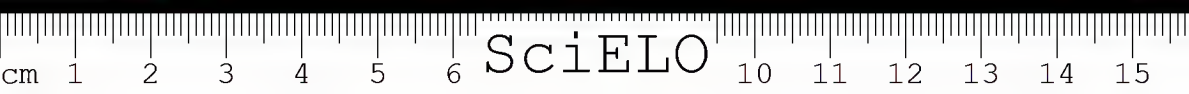


for reasons of objectivity and testability. The other two are also subject ultimately to the test of phylogeny as well.

Among the advanced snakes, analyses of parallelism have foundered for lack of good estimates of the phylogenetic relationships among taxa. Two of the venomous taxa, Viperidae and Elapidae, have traditionally been recognized only by the possession of either solenoglyphous or proteroglyphous dentition, respectively. For example, of a variety of features used by McDowell (1968) to diagnose the family Elapidae, only three unequivocally characterize members of this family, and two of these are aspects of the venom delivery system: (1) proteroglyphy, and (2) venom gland compressor divided into dorsal and ventral portions by the venom gland, and not attached to the cutaneous fold at the corner of the mouth. This second feature, as well as the third feature mentioned by McDowell, Harderian gland confined to the orbit, have been shown to be variable within the family by Savitzky (1978). Thus, there has been a decided tendency to define higher taxa of advanced snakes by the presence or absence of a particular suite of morphological characteristics associated with venom delivery. [Underwood (1967) used a number of other features to describe the venomous taxa, but it is unclear which will unambiguously characterize them].

Rigorous phylogenetic reconstruction requires that taxa be arranged in an explicit hierarchical fashion according to the evolutionary relationships of the taxa involved. With regard to the relationships among the traditionally recognized advanced snake taxa, two are usually characterized only by a particular suite of morphological features associated with venom delivery which are unique to each (Viperidae and Elapidae), and the third (Colubridae *sensu lato*) by the lack of such specialized features. Therefore, there appear to be no unambiguous data which will unite two or more of these (or subdivisions thereof) to the exclusion of the third. The question of whether front-fanged venom delivery systems have evolved in parallel thus becomes unanswerable because parallelism must always be analyzed with reference to a specific (implicit or explicit) phylogenetic hypothesis. In the case under consideration, since the features used to define groups are those for which we wish to interpret the evolutionary history, the question of parallel evolution cannot be resolved until other systems are investigated.

The work of Haas, Kochva, and their colleagues (summarized in Kochva, 1978) on gland structure and compressor muscle homologies clearly argues for a basic separation of the proteroglyphous and solenoglyphous lineages, but the case for association of one group with the Colubridae as a whole, or with a single lineage of colubrids, is not strong, and most workers implicitly accept one hypothesis over another without subjecting either to a rigorous test [for example, Marx and Rabb (1972, p. 6) use the Colubridae as an outgroup to the venomous taxa in their phyletic analysis of morphological characters, thereby *assuming* a particular phylogeny *a priori*]. In this regard, the work of Mosauer (1935) and Auffenberg (1958, 1961) on trunk musculature, and Kochva (1978) on salivary glands indicating derived features shared by elapids and colubrids, is promising, but needs to be examined in a broader array of taxa.



On the other hand, most studies which place little weight on the venom delivery system for phylogenetically useful characters (Burgeois, 1965; McDowell, 1968; Savitzky, 1978) proceed by pointing out similarities in other features (e.g., shape and nature of articulation between maxillary and ectopterygoid bones, position of Harderian gland, presence or absence of posterior vertebral hypapophyses, color pattern) between these problematic taxa and other (colubrid) groups. A difficulty with this approach is that, because of parallelism, it is possible that these kinds of comparisons will lead to erroneous hypotheses of relationships. Similarities due to common ancestry must be unambiguously separated from those due to homoplasy. For example, a fossorial mode of life is widely accepted to impart similar morphologies in diverse groups of snakes (Inger and Marx, 1965); yet, three of the postulated cases of parallelism in venom delivery systems, *Atractaspis*, *Homoroselaps*, and micrurines, involved genera exhibiting derived morphologies associated with fossoriality. A well-founded argument for why there should be parallelism in venom delivery systems, but not in the many other morphological features cited as evidence of common ancestry in many of these taxa, does not seem to exist.

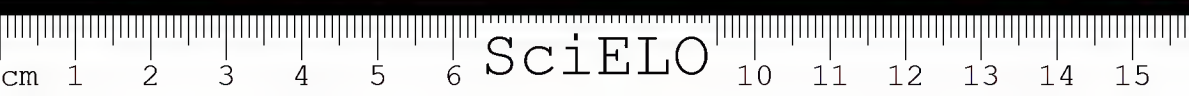
An implicit assumption of some of these studies (e.g., Savitzky, 1978) is that, because specialized venom delivery systems are adaptive, they should arise more often in parallel than other features. There is no theoretical justification for this assumption, and I suggest that specific structural configurations in such complexes (and their corresponding functional properties) may well be unique to particular lineages. This property has been noted for other complex character associations with regard to their distribution among lineages (Liem, 1973; Lombard and Wake, 1977; Russell, 1979). For example, Lombard and Wake (1977) studied the structure-function relationships among components of the complex tongue-projection apparatus in plethodontid salamanders. In three distinct lineages specialized for long-distance projection they found that each lineage exhibited specific arrangements of the elements of the apparatus which differed in their functional properties from those of other lineages. That these arrangements were evolved in parallel was suggested by structural differences which were discordant with the hypothesized phylogeny of the group. In such cases, functional parallelism is perhaps expected, but detailed structural parallelism is not. Thus, parallelism in complex morphological units can be detected by detailed comparisons of the structure and function of such features, and by their congruence with robust estimates of the phylogeny of the groups involved. Such studies have been carried out on the venom delivery systems of *Atractaspis* (Kochva *et al.*, 1967; Kochva, 1978), *Homoroselaps* (Kochva and Wollberg, 1970), and micrurines (Savitzky, 1978). *Atractaspis* was found to differ in gland structure and histochemistry from typical viperids and elapids, while the structure of the venom glands and associated muscles of *Homoroselaps* and micrurines conformed to that of typical elapids. [McDowell (1968) cited the undivided nature of the venom gland compressor in *Homoroselaps* as a character separating this genus from all elapids; Savitzky (1978), however, reports an undivided gland compressor in several species of the Oriental elapid

genus *Calliophis*; therefore this character cannot be considered diagnostic of the Elapidae]. In none of these studies have the details of venom gland and muscle morphology required an association with the colubrid groups from which these snakes were postulated to be derived.

The presumed extensive parallelism in advanced snakes causes two further, but related problems in the way evolutionary scenarios concerning the venomous snakes have been constructed (these are discussed in a more general context by Lauder, 1981): (1) it is sometimes assumed that annectant forms will exist among extant snakes which will show the transitional evolutionary stages between particular phenotypes (Bourgeois, 1965; McDowell, 1968; Savitzky, 1978). I have already discussed this problem above with reference to the relationships of micrurines and *Atractaspis*, where it is possible to show similarities of both of these groups to presumed ancestral (more generalized) groups. The problem is also noted in many attempts to align dental modifications into morphoclines (e.g., Bourgeois, 1965; Marx and Rabb, 1972) by assuming particular transformation series.

Perhaps the classic example of the extension of this idea are discussions of the relationships of the New World colubrids *Xenodon* and *Heterodon*, and their asserted intermediacy in the evolution of viperid dentition (Anthony, 1955; Kardong, 1979). Both *Xenodon* and *Heterodon* have greatly elongated posterior maxillary teeth that are saber-like in form. Viperid dentition was suggested to be derived from such dentition by shortening of the maxillary bone and the development of a canal in the fang (Anthony, 1955), leading to the designation of these colubrids as representative of a "protoviper" stage (Weaver, 1965; Kroll, 1976; Kardong, 1979). As such, this concept is an untestable construct, and yields practically no understanding of the evolution of the viperid venom apparatus. Indeed, it assumes that we already know what that evolutionary history was. While there is good evidence from comparative embryology for the homology of front fangs and venom glands in vipers to rear fangs and Duvernoy's gland in colubrids (Kochva, 1978) we currently have no basis at all for inferring that one or another morphotype represents the "protoviper" stage. In other words, all opisthognathous morphologies represent equally plausible ancestral morphologies for the evolutionary precursors of front fangs. The existence of intermediate morphologies among members of the extant fauna does not justify the conclusion that these are evolutionary intermediates. Such recognition requires a prior, corroborated hypothesis of the phylogenetic relationships among the taxa concerned.

This point has been discussed extensively by Dullemeijer (1974) and Lauder (1981). Both authors recognize the value of morphological series in studying morphological and functional patterns, but emphasize their inadequacy in constructing phylogenetic hypotheses: "Idealistic series do not necessarily indicate evolutionary series. A derivation of evolution from recent material always needs an additional argument to place the animals in a certain order." (Dullemeijer 1974, p. 207). The additional argument may take the form of an explicit phylogenetic hypothesis, which can serve as a point of departure for the analysis of ancestral morphologies (see Lauder, 1981).



(2) There is generally no basis for inferring the factors responsible for producing or maintaining particular feeding adaptations. A common interpretation in the literature is that selection pressures favor the initial elaboration of enlarged posterior maxillary teeth because of their supposed efficacy in subduing prey or in performing some other feeding function (Savitzky, 1978; Kardong, 1979). These are then presumably further modified by selection to result in more specialized front-fanged venom delivery systems. While I do not suggest that selection has no role in the evolution of these features, it is usually used as an *ad hoc* explanation for why certain structures exist, and, indeed, why there is parallelism in certain features (e.g., Kardong, 1979 for opisthogyphy; Savitzky, 1978 for proterogyphy). Circumstantial evidence suggests that there is unlikely to be a global selective basis of opisthogyphy, for this morphology is found in snakes living in all environments, and ingesting a variety of prey types (e.g., Bailey, 1966). Similarly, we cannot assume that front-fanged venom delivery systems are subject to extensive parallelism because of presumed selection pressures operating on a widespread ancestral morphology (i.e., opisthogyphy). For further general discussion of this problem see Gaffney (1979) and Lauder (1981).

Finally, how do we attack the problem of parallelism in front-fanged venom delivery systems? It should be clear from the foregoing that detailed and explicit phylogenetic hypothesis are needed, and that these must be derived from a methodology utilizing as few *a priori* and *ad hoc* assumptions as possible. Thus, *assumptions* about parallelism and the evolutionary mechanisms producing it should be eliminated as apriorisms in phylogenetic studies; rather, illumination of these processes should come from well-constructed and tested hypotheses of relationships. It is perhaps most reasonable in the construction of the phylogenetic hypothesis to start with the assumption that parallelisms are rare and to recognize them as they are *required* by a specific hypothesis.

Therefore, attention should be directed to the development of a well-corroborated (*sensu* Nelson, 1979) explicit phylogenetic hypothesis for the cladistic relationships among major groups of advanced snakes. With such a hypothesis in hand, then we may begin to investigate objectively the more interesting question of whether there has, in fact, been parallel evolution in front-fanged venom delivery systems, and by what mechanisms the biochemical and morphological manifestations of these systems have arisen evolutionarily.

I am not convinced that a rigorously cladistic methodology (*sensu* Hennig) is the most fruitful approach to this problem, for such parsimony approaches require that parallelisms and evolutionary reversals be minimal (see Felsenstein, 1978), an assumption that does not seem realistic given our current understanding of the evolutionary biology of snakes. Yet such attempts should be made, for the extent of parallelisms should be immediately obvious with such methods. Phylogenetic components analysis (Nelson, 1979; Nelson and Platnick, 1981) offers a potentially powerful method of phylogenetic analysis which might be profitably applied to the advanced snakes. It should be noted that this methodology requires neither assumptions about the directionality of evolution

nor the delineation of primitive and derived character states. In addition, chance association of taxa in a cladistic hypothesis can be separated from those likely to be due to common ancestry. Finally, molecular approaches, because of their recognized independence from morphological criteria (Wilson *et al.*, 1977), offer extremely valuable means of formulating and testing phylogenetic hypotheses, and may be expected to provide critical insight in cases where parallelism in morphology proves very common.

CONCLUSIONS AND PROSPECTS

There is an increasing awareness of the role that architectural and historical constraints play in determining the major morphological ground-plans exhibited by particular lineages during phylogeny (Gould and Lewontin, 1977; Gould, 1980). Under the view that such constraints may strongly influence the morphological patterns produced during the evolution of a particular lineage (see Gould, 1980 for discussion), major reorganizations of structure are expected to be rare and to conform to patterns modulated by ancestral structure. Thus, major phyletic lines are expected to share a fundamental design, with further minor modifications exhibited among their members. Precise replication of such major adaptive Baupläne involving numerous morphological features by parallel evolution is expected to be infrequent, for this requires the identical modification of many structures. Moreover, the outcomes are constrained by inherited developmental sequences, making precise replication unlikely among widely divergent lineages. In fact, good examples of such detailed parallelism appear to be quite rare.

Proteroglyph and solenoglyph venom delivery systems in snakes represent major structural designs in the feeding apparatus of advanced snakes. Attainment of either of these conditions requires evolutionary changes in the morphology of the jaw apparatus and dentition, oral glands, and the musculature associated with these features, as well as changes in the biochemical synthetic pathways of oral gland secretory products. Such specialized form-function complexes should represent fundamental structural and functional attributes of particular lineages (e.g., cichlid pharyngeal jaws; Liem, 1973), and parallelism in such systems might be expected to be rare. Parallelism, however, can be detected by detailed comparisons among lineages of the morphologies involved, in which case multiple configurations of the system are expected (see Lombard and Wake, 1977; Russell, 1979). Multiple evolution of particular functions is not, therefore, generally accompanied by detailed structural parallelism, but rather by different morphological patterns. Thus, the venom delivery components themselves should provide some of the primary evidence for parallelism in this system.

Kochva and Wollberg (1970) and Kochva (1978) note that the available information on the structure and function of the venom delivery systems among venomous snakes supports the conclusion that this feature shows both familial consistency and specificity in design; that is, the observed number of ways in which venom delivery systems in



snakes are constructed is very limited (the few data available on the structure of venom proteins also support this contention; see Lee, 1979). Among the front-fanged venomous snakes Kochva and Wollberg note only three types: the solenoglyph types represented in *Atractaspis* and typical vipers, and the proteroglyph type represented in all elapids (including *Homoroselaps* and *Micrurus*). I have summarized evidence above that these three groups represent the only advanced snake taxa for which adequate data exist upon which to suggest parallelism in the evolution of front-fanged venom delivery systems. In no case do I believe there is sufficient evidence suggesting the evolution of any of these systems from within living colubrid lineages (see also Kochva and Wollberg, 1970).

The problem remains as to whether the venom delivery systems seen in *Atractaspis*, viperids, and elapids represent true parallel acquisitions of simply various elaborations of a commonly inherited ancestral design. Another way of stating this is "Do the colubrids represent an outgroup to the front-fanged venomous taxa among advanced snakes?" The answer to this question relies on the acceptance of one or another phylogenetic hypothesis, none of which are robust under the criterion of being corroborated by numerous lines of evidence. We may look forward to a resolution of this problem with increasing evidence from molecular and morphological data, and from the application of rigorous phylogenetic methodology to those data.

Some goals for future research which are suggested by the foregoing discussion are:

(1) Attempts need to be made to define major lineages of advanced snakes on the basis of derived characters other than those associated with dentition and jaw apparatus. The phylogenetic hypothesis which result will provide the strongest means of testing hypothesis of parallelism in the venom delivery systems. Tests of particular phylogenetic hypothesis should be made using as many and varied comparative data as possible.

(2) Most of the focus in the literature on the evolution of snake venom delivery systems has been on dentition, gland structure, and muscle arrangements. Incorporation of basic information on venom components would greatly enhance our understanding of the *raison d'être* for these other features. Most of these data are scattered in the pharmacological and medical literature (see Lee, 1979) and need to be viewed from a phylogenetic perspective. We currently have the most detailed molecular data on elapid toxins (see discussion and references in Strydom, 1979). Extension of these data to the problematic elapid taxa I have discussed (*Homoroselaps* and micrurines) would be most welcome. In addition, our knowledge of the structure and function of viperid, and especially colubrid venom components, is notably sparse. Initial efforts on these groups promise significant insights into our concepts concerning the evolution and biochemical specialization of venom glands.

(3) We need information on the biological roles of snake venoms and venom components in natural prey items. Reports of toxicity in

experimental animals or humans contribute little or nothing to our understanding of the ecological and evolutionary significance of venom function. Such studies may elucidate the question of whether particular venom types or components are associated with particular prey types, ecological circumstances, or phylogenetic lineages.

Snake venom delivery systems represent one of the most specialized feeding apparatuses among vertebrates. A detailed and comprehensive understanding of the evolution of these systems should contribute to a general appreciation of pattern and mechanisms associated with the evolution of such complex morphological and biochemical adaptations. A resolution of the conflicting phylogenetic hypothesis that exist for the relationships among the venomous taxa will be the crucial first step in the unraveling of the history of this most interesting evolutionary innovation.

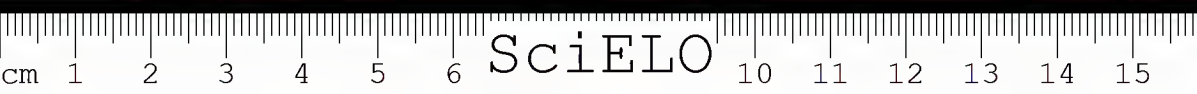
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SERPIENTES VENENOSAS DE CENTRO AMERICA

Distribución, características y patrones cariológicos

Róger BOLAÑOS *

RESUMEN: El trabajo presenta una visión panorámica de las serpientes venenosas de Centro América (Familias Hydrophidae, Elapidae y Viperidae), señalándose nuevas localidades para *Lachesis muta* y *Bothrops picadoi*. Se comenta también sobre la importancia médica de las distintas especies. Se muestran, además, los patrones cariotípicos de diez especies de Viperidae, cuatro de *Micrurus* y el de *Pelamis platurus* y se discuten posibles relaciones filogenéticas así como implicaciones taxonómicas.

UNITERMINOS: Serpientes venenosas; Centro América; Distribución geográfica; Cariotipos.

INTRODUCCION

El istmo centroamericano está formado, desde un punto de vista político, por siete pequeños países que conectan dos grandes masas continentales: Norte y Sur América (Fig. 1); sin embargo, desde un punto de vista biológico, parte del sur de México y del norte de Colombia deben ser considerados como parte de la zona. A pesar de eso, en la presente revisión únicamente será considerada la fauna de ofidios comprendida dentro de los límites políticos de la región.

La herpetofauna de América Central no solamente es muy abundante sino también, diversa; con base en diferentes listas publicadas se puede concluir que el suborden Serpentes está representado por no menos de 180 especies, agrupadas en cinco familias principales (1). Boidae, Colubridae, Hydrophidae, Elapidae y Viperidae. La primera incluye serpientes no venenosas — *sunsus strictus* — las Boas, cuya dentición es aglifa. Colubridae incluye algunas aglifas, pero también un número considerable de opistoglifas, técnicamente venenosas; a pesar de que un número considerable de mordeduras es producido por miembros de esta familia, muy pocos casos de envenenamiento han sido demostrados y todos los pacientes presentaron una sintomatología muy leve (Johanbocke, 1974; Minton,

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(1) Se conocen tres familias más, constituidas por cinco especies de serpientes ciegas, raras y sin importancia médica.



1979); este hecho contrasta con la situación en Africa, en donde serpientes opistoglifas son responsables por accidentes severos, incluso letales (Visser & Chapman, 1978); por razones prácticas, consideraremos esta familia como integrada por especies no venenosas. Hydrophidae está representada por un género con una sola especie, la pelágica serpiente de mar, *Pelamis platurus*, presente en las aguas del Pacífico de los seis países que tienen costas en este litoral. Elapidae (considerada por algunos autores como Micruridae), está representada por un solo género: *Micrurus*, con numerosas especies; como *Pelamis*, son proteroglifas y producen un potente veneno de efecto neurotóxico; son conocidas como serpientes de coral y a pesar de ser muy comunes en ciertas regiones, la frecuencia de sus accidentes es baja (menos del 2 por ciento) principalmente debido al pequeño tamaño de sus colmillos (1 a 2 mm) y al pequeño ángulo de abertura de su boca. La taxonomía de este grupo es un tanto ambigua; sin embargo, por lo menos pueden identificarse 14 especies bien descritas (Minton *et al.* 1970; Roze, 1970; Hoge & Romano, 1971) (Cuadro 1). Las serpientes más importantes desde el punto de vista médico que se encuentra en la región pertenecen a la familia Viperidae, subfamilia Crotalinae, siendo responsables por más del 85 por ciento de todos los accidentes y por el 99 por ciento de todas las defunciones; cuatro géneros se encuentran en Centro América: *Agkistrodon*, *Crotalus* y *Lachesis*, cada uno con una sola especie, y *Bothrops* con 12 (Cuadro 2).



Fig. 1. Mapa político de Centro América.

CUADRO 1

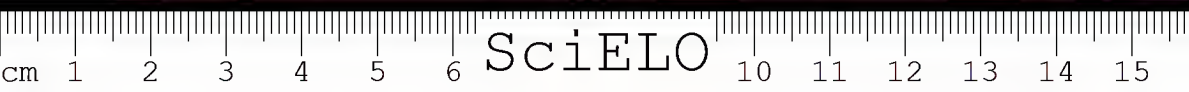
Distribucion de serpientes venenosas de las familias Elapidae e Hydrophidae en Centro America

Familias y especies	Guatemala	Belice y Honduras	El Salvador	Nicaragua	Costa Rica	Panamá
ELAPIDAE						
Anillos negros en triadas						
<i>M. ancoralis</i>	—	—	—	—	—	+
<i>M. dissoleucus</i>	—	—	—	—	—	+
<i>M. elegans</i>	+	—	—	—	—	—
Tricolores						
<i>M. alleni</i>	—	—	—	+	+	+
<i>M. browni</i>	+	—	—	—	—	—
<i>M. clarki</i>	—	—	—	—	+	+
<i>M. diastema</i>	+	+	—	—	—	—
<i>M. hyppocrepis</i>	+	—	—	—	—	—
<i>M. latifasciatus</i>	+	—	—	—	—	—
<i>M. nigrocinctus</i>	+	+	+	+	+	+
<i>M. rautanus</i>	—	+	—	—	—	—
<i>M. stewarti</i>	—	—	—	—	—	+
<i>M. stuarti</i>	+	—	—	—	—	—
Bicolores						
<i>M. mipartitus</i>	—	—	—	+	+	+
HYDROPHIDAE						
<i>P. platurus</i>	+	+	+	+	+	+

FAMILIA HYDROPHIDAE

Género *Pelamis* (*P. platurus*)

Nuestra serpiente de mar, con una distribución que va desde Baja California hasta el norte de Chile, es muy abundante en el litoral durante ciertas épocas del año, sin embargo, ningún accidente humano ha sido registrado hasta la fecha. El Dr. A.T.Tu (1976) colectó en las costas de Costa Rica, en solamente tres semanas, más de 3000 especímenes para sus estudios toxinológicos. Esta especie difiere de otras serpientes marinas en vivir en aguas limpias y mantenerse principalmente en la superficie, la mayoría de las veces en grupos numerosos. Su coloración básica incluye tres colores: negro en el dorso, amarillo brillante lateralmente y castaño claro en el vientre, existiendo arreglos principalmente en cuanto a la interrelación de las bandas; un tipo totalmente amarillo ha sido descrito en las aguas de Centro América (Bolaños *et al.*, 1974) con una frecuencia



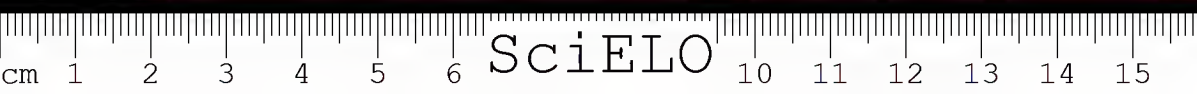
sumamente baja. El hecho de que ningún accidente ha sido descrito puede estar relacionado con su comportamiento poco agresivo y su preferencia por aguas limpias; sin embargo, cuando ella es capturada, atrapada en redes de pescadores o cuando se vara en las playas y es manipulada imprudentemente, bien podría causar un accidente, tal vez de consecuencias severas como resultado de su potente veneno neurotóxico. Afortunadamente los antivenenos producidos en Australia y Japón, a pesar de que son específicos para otros géneros de serpientes marinas, neutralizan efectivamente su veneno, al menos en animales de laboratorio.

CUADRO 2

Distribucion de serpientes venenosas de la familia Viperidae en Centro America

Géneros y especies	Guatemala y Belice	Honduras	El Salvador	Nicaragua	Costa Rica	Panamá
AGKISTRODON						
<i>A. bilineatus</i>	+	+	+	+	+	—
BOTHOPODS						
Terrestres						
<i>B. asper</i>	+	+	+	+	+	+
<i>B. godmani</i>	+	+	+	+	+	—
<i>B. lansbergi</i>	—	+	—	—	—	—
<i>B. nasutus</i>	+	+	?	+	+	+
<i>B. nummifer</i>	+	+	+	+	+	+
<i>B. ophryomegas</i>	+	—	+	+	+	+
<i>B. picadoi</i>	—	—	—	—	+	+
<i>B. punctatus</i>	—	—	—	—	—	+
Arborícolas						
<i>B. bicolor</i>	+	—	—	—	—	—
<i>B. lateralis</i>	—	—	—	—	+	+
<i>B. nigroviridis</i>	+	+	?	?	+	+
<i>B. schlegeli</i>	+	+	+	+	+	+
CROTALUS						
<i>C. durissus</i>	+	+	+	+	+	—
LACHESIS						
<i>L. muta</i>	—	—	—	—	+	+

El cariotipo de *Pelamias platurus* fue descrito por nosotros recientemente (Gutiérrez y Bolaños, 1980), estando compuesto por 20 macrocromosomas y 18 microcromosomas, para un número diploide de 38 cromosomas. Una pequeña constricción secundaria se aprecia en el cuarto par de autosomas. En las hembras un par de cromosomas se muestra ligeramente heteromórfico, siendo identificados como ZW; ambos son meta-



céntricos, sin embargo, uno de ellos es más pequeño y con el centrómero en una posición más submediana que el otro. Encontramos también en esta especie una mayor proporción de cromosomas acrocéntricos que en el resto de especies de la subfamilia que hasta el momento han sido objeto de estudio, lo que sugiere que *P. platurus* presenta un cariotipo más primitivo que las demás. En el Cuadro 3 se presentan, comparativamente, algunas características cariológicas que han sido demostradas en estudios con serpientes marinas, de donde se desprende — de acuerdo con Singh (1972) — que la evolución cromosómica en la subfamilia Hydrophinae debe haber ocurrido a expensas de los macrocromosomas, puesto que todas las especies estudiadas presentan 18 microcromosomas. *Laticauda semifasciata* (Laticaudinae) presenta un cariotipo claramente distinguible de aquellos de Hydrophinae.

FAMILIA ELAPIDAE

Género *Micrurus* (serpientes de coral)

Está representado en Centro América por 14 especies (Cuadro 1), con numerosas subespecies, algunas muy bien definidas gracias a su aislacionismo geográfico. Esas especies pueden agruparse en tres categorías en cuanto a su coloración: 1. Con anillos negros en triadas, como son los casos de *M. elegans*, de la porción sur del istmo, y *M. ancoralis* y *M. dissolucus* del sur. 2. Tricolores, en donde los anillos rojo y negro están siempre separados por un anillo claro (amarillo o blanco); en esta categoría se agrupan la mayoría de las especies, siendo el prototipo *M. nigrocinctus*, la Coral Centroamericana, la más frecuente en todos los países y la de mayor importancia médica. 3. Por último, el tipo en donde predominan dos colores, blanco y negro en secuencia, pero con la cabeza y la cola con escamas rojas, o rojo y negro; en esta categoría hay una sola especie *M. mipartitus*, exclusiva del sur del istmo. En la Fig. 2 se presenta un ejemplar adulto de *M. nigrocinctus*. De las diversas subespecies de *M. nigrocinctus* que han sido consideradas recientemente en la literatura, en dos de ellas, *M. n. nigrocinctus* (= *M. n. melanoccephalus*) y *M. n. mosquitensis*, Savage y Vial (1973) sugieren la eliminación del trinomio en vista de lo que ellos consideran — con un criterio morfológico — tipos intermedios entre ambas poblaciones en las zonas donde se traslapan. Nuestros estudios cariológicos indican un claro patrón diferencial entre ambas poblaciones, a expensas de los microcromosomas, sin que se presenten cariotipos híbridos que podrían sugerir entrecruzamiento (Gutiérrez y Bolaños, 1981).

Los cariotipos de tres especies de *Micrurus*: *M. mipartitus*, *M. alleni* y *M. nigrocinctus*, esta última en sus dos subespecies (*M. n. nigrocinctus* y *M. n. mosquitensis*), han sido investigados por Gutiérrez y Bolaños (1979). Los autores demuestran un intenso polimorfismo cromosómico, a diferencia de lo que ocurre en Viperidae, como se observa en los idiotipos que se presentan en la Fig. 3. Es conveniente hacer notar, nuevamente, que los cariotipos de *M. n. nigrocinctus* y *M. n. mosquitensis* se diferencian claramente por el número de microcromosomas (12 y 14 respectivamente) y por la posición del centrómero en el octavo par de autosomas.

CUADRO 3

Resumen de los cariotipos que han sido descritos en serpientes marinas

Subfamilias y especies	2n (macro- + microcromosomas)	Constricción	Heteromorfismo sexual
LATICAUDINAE			
<i>Laticauda semifasciata</i>	38 (18+20)		
HYDROPHINAE			
<i>Pelamis platurus</i>	38 (20+18)	Si	ZW
<i>Hydrophis ornatus</i>	32 (14+18)	Si	ZW
<i>Hydrophis spiralis</i>	32 (14+18)	No	ZW
<i>Kerilia jerdoni</i>	32 (14+18)	Si	?
<i>Hydrophis cyanocinctus</i>	0 32 (14+18); 0 33 (15+18)	Si	ZW ₁ W ₂
<i>Enhydrina schistosa</i>	0 32 (14+18); 0 33 (14+19)	Si	ZW ₁ W ₂
<i>Hydrophis fasciatus</i>	0 34 (16+18); 0 35 (17+18)	No	ZW ₁ W ₂
<i>Microcephalophis gracilis</i>	0 34 (16+18); 0 35 (17+18)	No	ZW ₁ W ₂

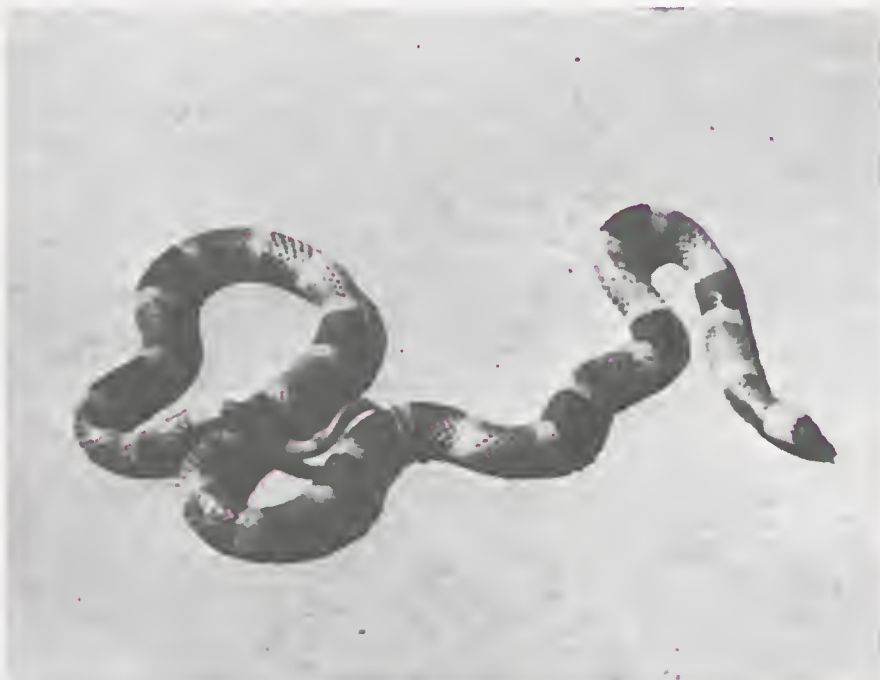


Fig. 2. *Micrurus nigrocinctus mosquitensis*

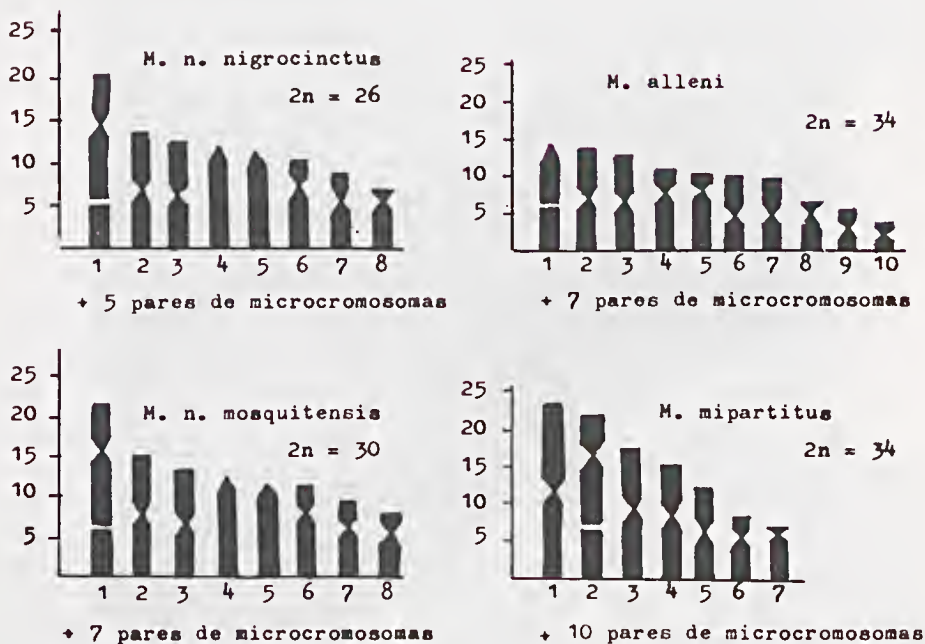


Fig. 3. Idiograma de los cromosomas de *Micrurus nigrocinctus*, *M. alleni* y *M. mipartitus*, según Gutiérrez y Bolaños (1979). El eje vertical corresponde al porcentaje del par en el genoma total; el horizontal representa el número del par.

Al estudiar en conjunto los cariotipos de todos los *Micrurus* que hasta el momento han sido publicados, se puede señalar que el par de cromosomas sexuales es el N.º 6, con cromosomas ZW, siendo el primero submetacéntrico y el segundo acrocéntrico y más pequeño. Además, que de todos los cariotipos hasta el presente estudiados, pareciera ser que el de *M. lemniscatus carvalhoi* (Beçak y Beçak, 1969) es el más primitivo pues todos sus macrocromosomas son acrocéntricos.

Inmunológicamente, hemos podido demostrar que los *Micrurus* pueden ser agrupados en categorías de acuerdo a la especificidad neutralizante de sueros antiofídicos frente a sus venenos. En el Cuadro 4 se muestran los grupos serológicos que hemos podido demostrar. Además, también hemos logrado preparar un suero multivalente, capaz de neutralizar todos los venenos, simplemente inmunizando caballos con una mezcla de venenos representativos de cada uno de los grupos anteriores (Bolaños *et al.*, 1978).

FAMILIA VIPERIDAE, SUBFAMILIA CROTALINAE

Género *Agkistrodon*

Agkistrodon bilineatus es la única representante de este género en Centro América. Es popularmente llamada Cantil o Castellana y se le encuentra desde Guatemala hasta Costa Rica, en la región semiárida del litoral del Pacífico. No tenemos conocimiento de accidentes por esta especie; sin embargo, al menos experimentalmente, su veneno es producido en cantidades suficientes como para causar un accidente de relevante magnitud. Son típicas en ella las escamas blancas que bordean su boca y dibujan líneas en su cabeza que asemejan una jáquima. En la Fig. 4 se muestra un ejemplar, procedente de Guatemala.



Fig. 4. *Agkistrodon bilineatus*. Probiación de Guatemala. Nótese la ornamentación de la cabeza mediante hileras de escamas blancas. (Foto cortesía de B. van den Brule).

Género *Crotalus*

Una sola especie, *C. durissus*, con una sola subespecie, *C. d. durissus*, se presenta en Centro América con una distribución idéntica a la de *A. bilineatus*: zonas bajas y semiáridas del Pacífico, entre Guatemala y Costa Rica, estando ausente en Panamá.

En un intenso estudio sobre accidentes bien comprobados en humanos causados por *C. d. durissus* (Bolaños *et al.*, 1980) pudimos demostrar que su envenenamiento no reviste la severidad de aquellos que producen sus congéneres en otras latitudes, pudiendo ser catalogados como moderados, aún en los casos más violentos; en ninguno de nuestros 21 pacientes pudo demostrarse efecto neurotóxico, como tampoco, comprometimiento renal. En la Fig. 5 se presenta un ejemplar adulto de la Cascabela centroamericana, los cuales pueden alcanzar un tamaño promedio de 1,35 m, con un cuerpo relativamente grueso, pero una cabeza bastante pequeña.



Fig. 5. *Crotalus durissus durissus*, Cascabela centroamericana.

Género *Lachesis*

Común en Panamá y Costa Rica, donde habita zonas selváticas de condición húmeda y muy húmeda. Su relación con el hombre no es frecuente, de ahí que los accidentes sean raros; sin embargo, en cuatro de ellos bien confirmados, y con tratamiento con suero específico establecido tempranamente (2 horas o menos de evolución), pudimos demostrar una mortalidad del 75 por ciento (Bolaños *et al.*, 1982). Hasta el momento una sola subespecie había sido considerada en Costa Rica y Panamá (Peters y Orejas-Miranda, 1970): *L. m. stenophrys* (Cope); sin embargo, recientemente hemos podido demostrar la presencia en Panamá de *L. m.*

muta (Linnaeus) (Martínez y Bolaños, 1982), en una zona en donde es posible que se presente una intergradación entre ambas poblaciones, la provincia de Darién, en la región limítrofe con la provincia de Panamá.

En la región del Pacífico lluvioso de Costa Rica (Península de Osa y zonas adyacentes) se presenta una población de *Lachesis* totalmente diferente en muchas características a *L. m. stenophrys* y que aún no ha sido descrita, a pesar de que Bolaños *et al.* (1978) ya señalaban diferencias en colorido, comportamiento y características inmunológicas de su veneno.

Dentro de los viperidios de Centro América esta serpiente es la única ovípara, siendo por lo general el número de huevos de 10 a 12, los que requieren una incubación de aproximadamente dos meses, dependiendo de la temperatura, y una humedad relativa cercana al 100 por ciento. La época de postura, al menos en Costa Rica, se encuentran entre Julio y Agosto, lo que corresponde a lo más intenso de la estación lluviosa.

La población del Pacífico de Costa Rica de *L. muta* difiere de *L. m. stenophrys* (Atlántico) y *L. m. muta*, primero en presentar un capuchón negro que recubre toda la parte superior de su cabeza y que se extiende lateralmente hasta la banda posocular, la cual enmascara, mientras que las otras presentan manchas discretas en mayor o menor número según la subespecie. Además, una notoria diferencia se presenta con el número de escamas ventrales; mientras en *L. m. muta* es mayor de 214 para los machos y de 226 para las hembras y en *L. m. stenophrys* menor de esas cifras (Peters y Orejas-Miranda, 1970), nuestra población del Pacífico se sitúa en el medio, con un rango de 214-216 para los machos. Difieren también en el colorido de su cuerpo, presentándose la coloración de fondo grisacea en *L. m. muta* y castaño amarillento en *L. m. stenophrys*, ambas con triángulos castaño oscuro, mientras que en la población del Pacífico de Costa Rica el color de fondo es amarillo y su ornamentación muy oscura, casi negra. En la Figs. 6 y 7 se muestran ejemplares de estas dos poblaciones de *L. muta* de Costa Rica, los cuales alcanzan dimensiones, en promedio, de 2 metros o más.

CUADRO 4

Grupos de venenos de *Micrurus* que presentan reaccion cruzada en pruebas de neutralizacion

Grupo serológico	Especie de <i>Micrurus</i>	Localización geográfica
1	<i>M. fulvius</i>	América del Norte
	<i>M. nigrocinctus</i>	Centro América
	<i>M. dumerili</i>	Sur América
2	<i>M. corallinus</i>	Sur América
	<i>M. frontalis</i>	Sur América
	<i>M. spixi</i>	Sur América
3	<i>M. alleni</i>	Centro América
	<i>M. mipartitus</i>	Centro y Sur América
4	<i>M. surinamensis</i>	Sur América



Fig. 6. *Lachesis muta stenophrys*. Población del Atlántico de Costa Rica.



Fig. 7. *Lachesis muta*. Población del Pacífico sur de Costa Rica.

Género *Bothrops*

Similarmente a la situación del género *Micrurus*, se presentan en Centroamérica *Bothrops* típicos del norte, cuya dispersión llega hasta Guatemala y típicos del sur, hasta Panamá, además de una población autóctona más numerosa (Cuadro 2). Desde el punto de vista médico son cuatro las especies que parecen tener mayor importancia: 1. *B. asper* (Fig. 8) responsable por más de un cincuenta por ciento de los accidentes ofídicos y por la casi totalidad de las defunciones; alcanza tamaños considerables con un promedio de 1,4 m y un máximo, observado por nosotros, de 2,2 m; produce la mayor cantidad de veneno de todas las especies Crotalinae de Centro América, con un promedio de 458 mg y un máximo de 1.530 mg de veneno seco (liofilizado) en ejemplares recientemente capturados (Bolaños, 1972). 2. *B. nasutus*, pequeña, terrestre, y productora de accidentes frecuentes pero de escasa importancia, debido a la pequeña cantidad de veneno capaz de inocular. 3. *B. schlegeli* y 4. *B. lateralis*, arborícolas de color predominante verde, cuya importancia principal estriba en el hecho de que provocan accidentes en los miembros superiores, principalmente en la mano, en donde una pequeña cantidad de veneno, como la que producen, es capaz de causar una disfunción con consecuencias importantes para la normal función del miembro. En las Figs. 9 y 10 se presentan ejemplares adultos de *B. schlegeli* y *B. lateralis*, ambas con dimensiones similares de aproximadamente 60 cm. En Costa Rica es muy frecuente una variedad de *B. schlegeli* de coloración totalmente amarilla que no se observa en otros países del área ni en Sud América. *B. bicolor* de Guatemala pareciera ser el equivalente ecológico de *B. lateralis* de Costa Rica y Panamá. Otros miembros del género no son relevantes desde un punto de vista médico puesto que sus accidentes no son frecuentes.



Fig. 8. *Bothrops asper*, ejemplar de 1,70 m.

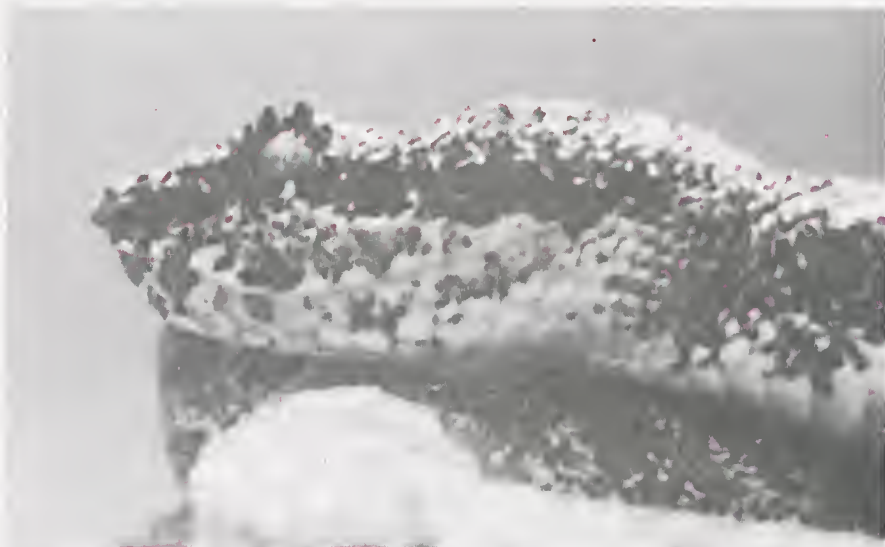


Fig. 9. *Bothrops schlegeli*, detalle de la cabeza. Nótese las escamas superciliares características de la especie.



Fig. 10. *Bothrops lateralis*. Se observan las típicas líneas amarillas longitudinales en la región látero-ventral, así como pequeñas líneas transversales en el dorso.

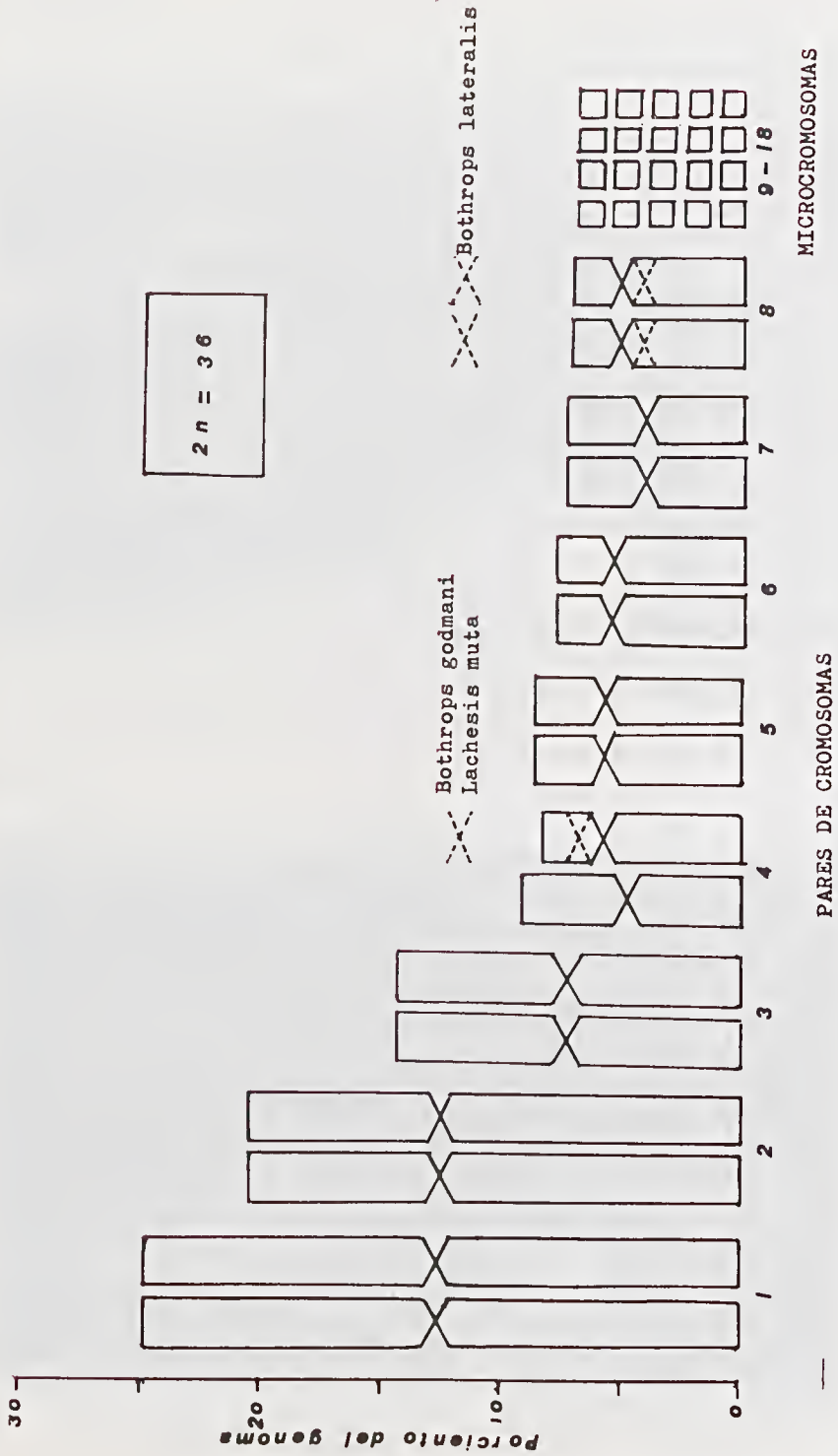


Fig. 11. Idiograma de los cromosomas de serpientes centroamericanas de la Familia Viperidae, según Gutiérrez et al. (1979).

Recientemente hemos podido demostrar diferencias notorias en efectos farmacológicos y patrones electroforéticos de veneno de diferentes poblaciones de una misma especie de *Bothrops*, como también diferencias entre recién nacidos y adultos de ejemplares de una misma población. Así por ejemplo, *B. asper* de la región atlántica de Costa Rica presenta un veneno más hemorragíparo y mionecrótico que los del Pacífico; estos últimos muestran mayor efecto proteolítico, siendo ambos similares en cuanto a mionecrosis, hemólisis indirecta y letalidad. Con respecto a las diferencias ontogénicas, los venenos de ejemplares recién nacidos son más proteolíticos, hemorragíparos, edematizantes y letales para el ratón, mientras que los adultos presentan mayor efecto hemolítico y mionecrótico (Gutiérrez *et al.*, 1980).

Un miembro de este grupo, *B. picadoi*, se conoce en la literatura como exclusivo de Costa Rica, con una distribución que se limita a montañas de baja altitud que se encuentran alrededor de la Meseta Central del país. Sin embargo, recientemente fue encontrada e identificada en zonas altas de la provincia de Chiriquí, Panamá, cerca de la frontera sur de Costa Rica (V. Martínez, comunicación personal), de tal suerte que su ámbito de extensión debe ser ampliado.

Los cariotipos de 10 especies de Crotalinae de Centroamérica han sido estudiados por Gutiérrez *et al.*, (1979) siendo todos ellos idénticos a los observados por Beçak (1965) y Beçak & Beçak (1969) para serpientes de la misma familia en Sur América, es decir, un número diploide de 36 cromosomas con 16 macro y 20 microcromosomas y con un heteromorfismo cromosómico de las hembras en el cuarto par (ZW). Fueron demostradas pequeñas diferencias en la posición del centrómero en algunos pares de macrocromosomas, pero sin implicación aparente en sentido evolutivo. Un diagrama de este cariotipo y sus diferencias entre especies se presenta en la Fig. 11.

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ABSTRACT: The paper presents a panoramic view of the poisonous snakes of Central America (Hydrophiidae, Elapidae, and Viperidae families), showing new localities for *Lachesis muta* and *Bothrops picadoi*. Comments are presented on the medical importance of the species. Also the cariological patterns of ten Viperidae, four *Micrurus*, and *Pelamis platurus*, with a discussion of some filogenetic relationships.

KEYWORDS: Poisonous snakes; Central America; Geographical distribution; Karyotypes.

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SciELO

PRELIMINARY REPORT ON THE MEDICAL IMPORTANCE OF *SICARIUS* (ARANEAE: SICARIIDAE) AND THE ACTION OF ITS VENOM

Gerald NEWLANDS *

ABSTRACT: Following a report of a person who suffered very serious tissue loss after being bitten by a spider which answered to the description of *Sicarius spatulatus* Pocock, I decided to investigate the matter. Specimens of *S. albospinosus* Purcell were used for envenomation experiments with rabbits in order to document the clinical signs and symptoms, histopathological, chemopathological and haematological consequences of the bite. In the laboratory the bite of *Sicarius* proved to be far worse than those of South African species of *Loxosceles* and the behaviour and distribution of these spiders is thus of relevance in terms of their epidemiological importance. Species of *Sicarius* occur in the less densely populated areas of South America and southern Africa. The restricted distribution in low human density areas means that human accidents are likely to be rare. The bite of *Sicarius* results in an intensely necrotic and haemorrhagic lesion locally and systemic symptoms attributable to disseminated intravascular coagulation.

INTRODUCTION

Spiders of the genera *Sicarius* and *Loxosceles* are closely related and share many morphological and behavioural similarities. Both are primitive six-eyed spiders with simple and similar male and female genitalia. Furthermore, species of both genera stridulate by the same unique mechanism (rub scrapers on the palpal femurs against stridulatory files on the outer surface of the chelicerae) and both spiders bury their egg sacs in sand (no other spiders do this). Accordingly, when a human accident was reported to me and involved considerable tissue destruction following a bite by a spider answering to the description of *S. spatulatus* Pocock and in an area where it is common, I decided to investigate the matter toxicologically.

To date, all the published accounts of *Sicarius* species have been of a taxonomic and behavioural nature. Of the 23 species currently

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accepted (Gerschman de Pikelin & Schiapelli, 1979) 15 were described between 1849 and 1900. It is clear that the genus needs revision, especially in South America where most of the species occur and where the published distributional records are out of date. Three works on the behaviour of South American species have been published (Levi, 1967; Levi & Levi, 1969 and Reiskind, 1965) but an extensive manual and computer search of the literature failed to reveal any clinical or toxicological studies on these spiders.

Zoogeographically, the disjunct distribution of *Sicarius* species in the arid parts of the widely separated Neotropical and Afrotropical regions is interesting (fig. 1). Clearly, ancestors of present day species were separated by continental drifting following the break-up of Gondwanaland in Cretaceous times. It is most unlikely that these primitive spiders could have been dispersed by any other means since the continental displacement. Spiderlings of sicarid species do not balloon as do many of the more advanced web-bound labidognath spiders such as *Latrodectus* species. Because of their xerophilous, rupicolous way of life, sicarids are extremely unlikely candidates for dispersal by the normal agencies such as accidental carriage with human trade goods and travel, with migratory animals or by rafting on driftwood, which are normally implicated in the intercontinental dispersal of invertebrates. Regarding the disjunct distribution of *Sicarius* in terms of continental displacement, there is one anomaly viz *S. utriformis* (Butler) recorded from the Galapagos Islands which are unrelated to continental drifting in that they are of relatively recent volcanic origin. To the best of my knowledge, *S. utriformis* is known only from the types described in Victorian times and it is possible that the record is inaccurate.

METHODS

The *in vivo* envenomation studies were conducted with the approval of the Witwatersrand University Animal Ethics Committee. Rabbits were given tetracycline antibiotics by subcutaneous injection 24 hours prior to envenomation and daily thereafter to reduce the chances of artefacts due to secondary infections. Hind quarters of adult Californian white rabbits were depilated by means of an electric shaver and a proprietary depilatory cream. Adult spiders were induced to bite at the centre of the depilated area by pressing the spider into contact with the rabbit's skin. As *Sicarius* bites with reluctance, the spiders normally had to be annoyed by pulling their pedipalps with fine forceps to induce biting. The clinical appearance of the skin was monitored and changes were photographed in colour and with Kodak High Speed Infrared Film using a Kodak Wratten Filter 87C over an electronic flash and a dark red filter over the camera lens. Infrared film was used to monitor extravasation in the upper and middermis. Blood samples for haematological and biochemical study were taken with a No. 23 (0,6mm) Butterfly disposable needle inserted into the median artery of the ear or by cardiac puncture with a No. 18 needle on a 50 cm³ syringe. Aliquots



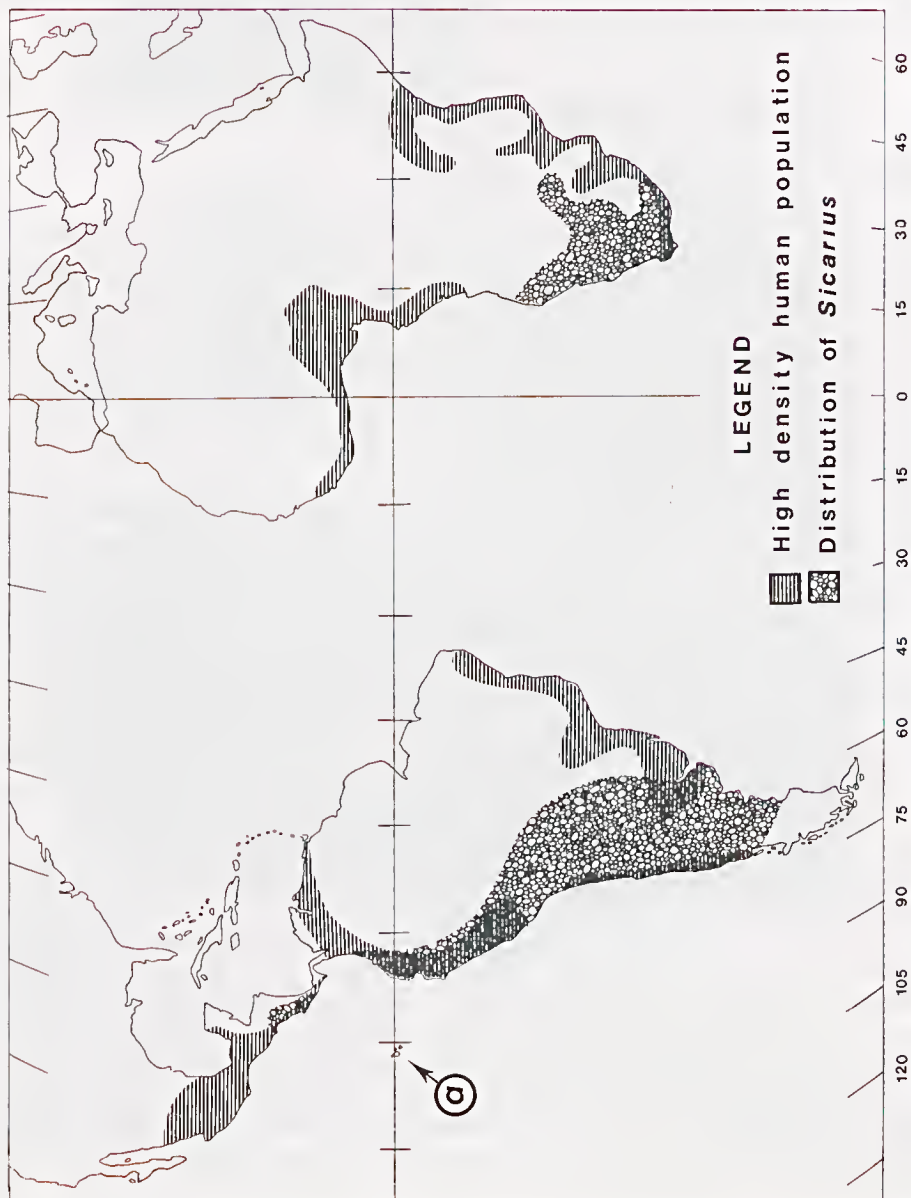
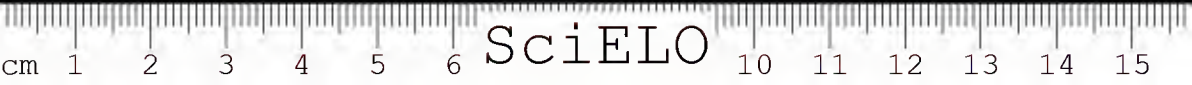


Fig. 1. Distribution of *Sicarius* species in relation to the high density human populations, viz more than 10 people per km². All areas where distributions over lap should be regarded as the most likely regions for human accidents with these spiders. The species *S. utiformis* (Butler) was described from the Galapagos Islands (a) in 1877.



for histological study were removed post-mortem in the usual way. The aliquots were machine processed and the sections were stained with haematoxylin and eosin. The majority of blood and serum samples were machine analysed as routine clinical specimens in the standard manner. A Beckman 1260 autoanalyser was used for the serum biochemistry screening. Venom was tested for proteolytic activity by the method of Rinderknecht *et al.* 1968 in which a hide powder azure was used as a chromogenic substrate.

Specimens of *S. albospinosus* for the study were collected beneath rocks in the Namib desert at Awasib, Tsondab vlei and Lüderitz during a field work expedition between February and March 1981.

EXPERIMENTAL RESULTS

Observed signs and symptoms of envenomation.

Ten experiments were conducted and the following is typical. Within 15 minutes, the first change observed was a small purplish discolouration of the skin at the bite site. By 20 minutes, a well defined 25mm wheal formed (fig. 3), the central area of which contained a diffuse purple zone of about 4mm at the bite site. Skin in the wheal area was of a distinctly glossy and reticulated texture quite markedly different from the surrounding area. Infrared photographs at this stage suggested slight dermal extravassation covering an area of about 5 by 11mm about the bite site.

By an hour after the bite, the glossy and reticulated skin zone had spread to about 20 by 30mm and the central haemorrhagic area was about 6 by 25mm and was much darker in colour. Infrared photographs depicted a marked increase in the dermal extravassation. After a further hour and a half, the lesion had increased in size by two or three millimetres and a dark central necrotic zone had formed. Five hours after the bite, a black eschar (8 x 15mm) had begun to form over the central area of the lesion and this was surrounded by a clearly haemorrhagic zone (15 by 20mm). Of significance at this stage was the fact that there was no evident oedema or erythema which are normally seen in cases of loxoscelism.

At seven hours, the clinical picture began to change, the eschar had become quite hard and the surrounding zone of haemorrhage was much darker in colour. The glossy reticulated appearance of the skin, characteristic of skin at the bite site for four or five hours after the bite, was no longer evident and an ecchymotic zone in excess of 50mm was clearly visible (fig. 4). Patches of skin damaged by the electric shaver and depilatory preparations were becoming conspicuous in the form of mildly haemorrhagic lesions. What appeared to be a scattered and barely perceptible macular rash was developing at this stage. Infrared photographs (fig. 5) confirmed that the central lesion was intensely haemorrhagic and circumscribed by an extensive area of ecchymosis.

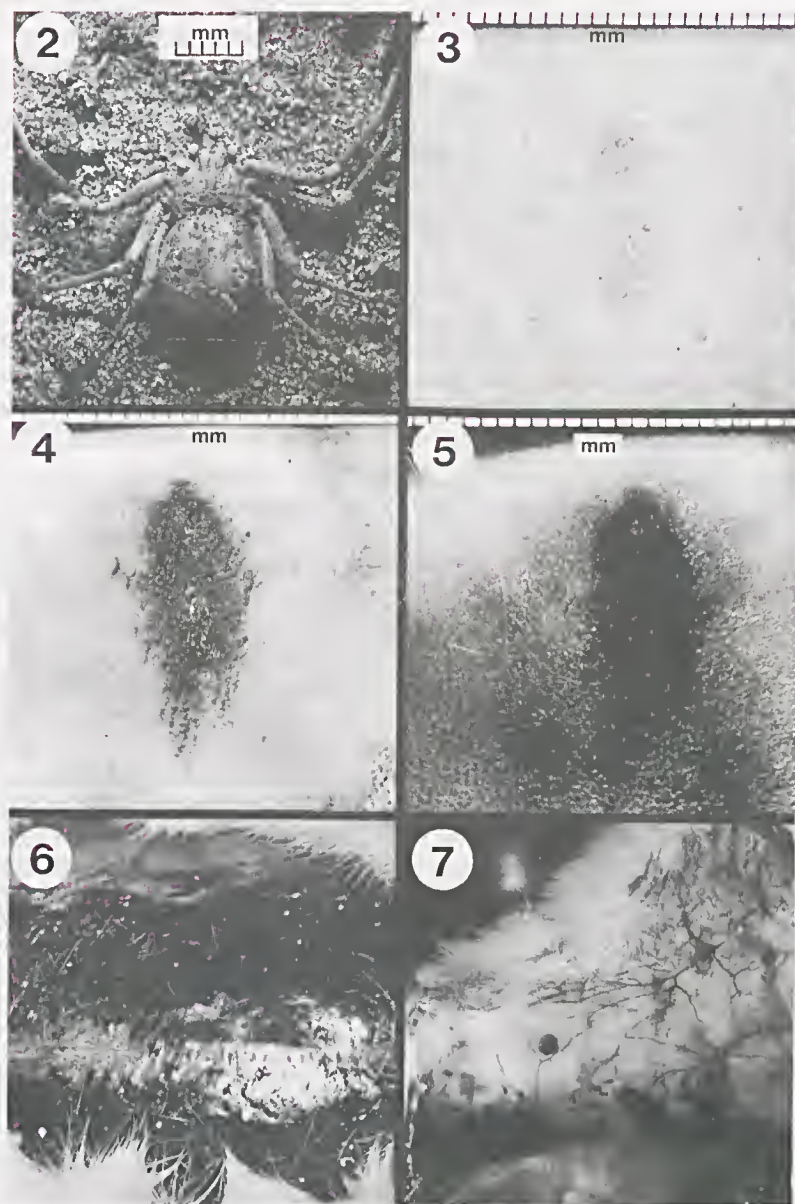


Fig. 2. Dorsal view of *Sicarius hahnii* (Karsch) 1878.

Fig. 3. Lesion on rabbit as seen 20 minutes after a *S. albospinosus* bite.

Fig. 4. Same lesion depicted in Fig. 3 but at 7 hours after the bite and showing haemorrhage, necrosis and eschar formation.

Fig. 5. Same lesion depicted in fig. 4 at the same time but photographed with infrared film to reveal the severe haemorrhage of the central lesion (black) surrounded by an extensive area of echymosis (dark grey area). The gravitational effect on the spread of the lesion is very evident.

Fig. 6. The extensively haemorrhaged subcutaneous abdominal wall of a rabbit which had died within 16 hours of a *Sicarius albospinosus* bite.

Fig. 7. Rabbit which was sacrificed 6 hours after a *Sicarius albospinosus* bite. Skin covering the abdominal region has been peeled back in order to reveal the widespread petechial haemorrhages of the dermis and abdominal wall in relation to the vascular system.

Most of the rabbits died within 4 to 16 hours, but in those which survived (possibly received milder bites), the central necrotic zone was depressed by 18 hours and surrounded by an extensive area of ecchymosis, erythema and oedema. The eschar sloughed in 9 days, leaving a crater up to 60mm across and revealing tremendous damage to the subdermal tissue and skeletal muscle. In rabbits, the lesion healed rapidly after the eschar had sloughed, provided no secondary infection was allowed to develop. In the early stages, the lesion was always found to be sterile, even when no prophylactic antibiotics had been administered. Proteolytic enzymes in the venom probably destroyed bacterial contaminants in the early stages.

Signs and symptoms seen in rabbits prior to death were those of collapse. Slight paralysis of the hind limbs, generalised cyanosis, shallow breathing and body temperatures as low as 34,7°C were measured. None of the rabbits showed signs of haematuria or haemoglobinuria. Death appeared to result from respiratory failure.

Post-mortem Findings

Autopsy examinations were conducted immediately after death in most cases. In two animals which had died a few hours before autopsy, the sub-dermal abdominal wall was found to be very extensively haemorrhaged (fig. 6). In all freshly dead rabbits, the abdomen and inside surface of the skin displayed widespread petechial haemorrhages associated with the vascular supply (fig. 7) which is suggestive of a disseminated intravascular coagulopathy (DIC). Further support for the diagnosis of DIC was forthcoming on examination of the systemic organs, many of which were petechially haemorrhaged. This systemic pathology was evident from about five hours after envenomation. Organs generally affected were the alimentary canal and mesenteries, kidneys, liver, spleen, lungs, heart and the subconjunctiva of the eye. During the autopsy, aliquots of systemic organs were taken for histological investigation.

Histological Findings

Skin punch biopsy aliquots removed from the lesion at the bite site three hours after envenomation, revealed early vasculitis accompanied by massive extravassations throughout the depth of the collagen layer. Very little inflammatory reaction and oedema could be detected at this early stage, a finding which contrasts markedly with those of South African loxosceline envenomation lesions.

By six hours after envenomation, the epidermis at the bite site had completely disappeared, probably due to a direct proteolytic effect of the venom. This lysed tissue overlaid a collagen layer which was intensely haemorrhaged and necrotic (fig. 8). Occasional polymorphonuclear leukocytes and eosinophils were seen throughout the dermis. The dissolution of the epidermis must have been the result of a proteolytic enzyme in the venom as this was too early after the bite to be an ischemic effect caused by the vasculitis. Studies conducted with hide-powder azure substrates confirmed that *Sicarius* venom has a strongly



proteolytic action. Other changes observed in the skin at six hours were, fibrin-thrombi clots partly occluding the lumens of blood vessels and necrosis of the muscle layers at the dermal-muscle interface (fig. 9). It must be stressed that as the skin and systemic organ aliquots were removed from the freshly dead rabbit, the fibrin-thrombi clots seen in most of the sections were not necessarily attributable to a diffuse intravascular coagulation syndrome.

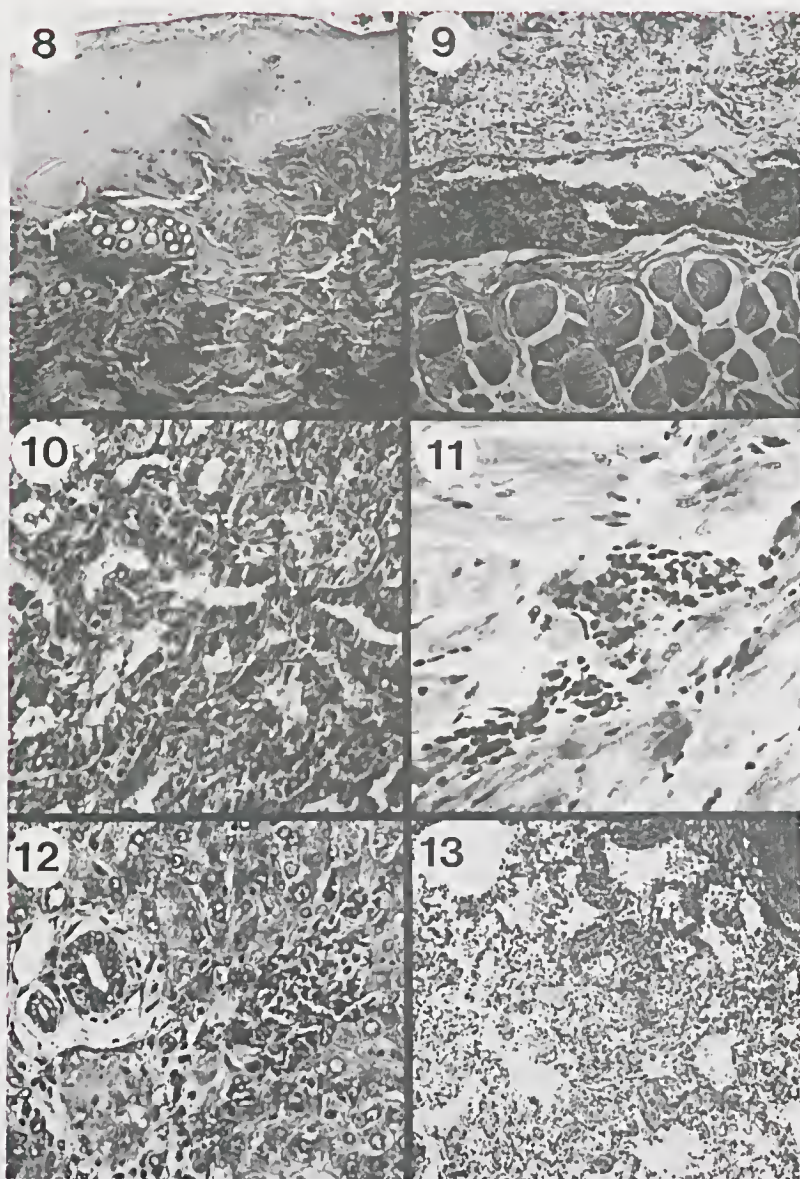
Changes seen in the kidneys after six hours were focal areas of inflammatory cells in the medulla, congested glomeruli and evidence of necrosis (fig. 10). No evidence of haemoglobin casts in the renal tubules could be detected. Vorse et al (1972) described haemoglobin casts in renal tubules in a fatal case of loxoscelism with disseminated intravascular coagulopathy. This finding was in keeping with the fact that no evidence of haemoglobin could be detected in rabbits which died within 12 hours of envenomation.

Petechial haemorrhages seen on the small intestine during autopsy proved to be slight extravassation of erythrocytes into the lamina propria. Changes in the spleen were found to be very slight congestion and a slight inflammatory infiltrate into the red pulp region accompanied by areas of necrosis with pycnosis and karyorhexis of the nuclei. Likewise, changes in the adrenal glands were not marked; slight extravassation of erythrocytes into the periadrenal fat accompanied by congestion were the only detectable abnormalities. The heart displayed areas of subendocardial haemorrhage and mononuclear cell infiltrates between the striated muscle of the heart giving rise to foci of interstitial myocarditis (fig. 11). Eosinophilic micro-abscess formation, small areas of necrosis and fibrin thrombi in the portal vessels were the main histological findings in the liver (fig. 12). Lungs of all the rabbits exhibited marked changes such as pulmonary oedema, widespread inflammatory cell infiltrates and areas of eosinophilic micro-abscess formation (fig. 13). Changes seen in the other organs were either slight such as the perivascular cuffing seen in the brain or possible artefact related to some other cause such as one rabbit which had a well formed granuloma in the cerebellum.

Serum biochemistry and haematological findings

Generally, the serum biochemical and haematological findings concurred with the histopathological findings. Higher levels of the circulating enzymes alkaline phosphatase, alamine transaminase (ALT) and aspartate transaminase (AST) suggest massive hepatocellular damage which was noted in the histology at an early stage (Table 1). Increases in the creatine phosphokinase (CPK) normally suggest muscle trauma and myocardial infarction and it is possible that skeletal muscle damage at the bite site, and the histological changes seen in the heart muscle (possibly due to DIC) are causes for the high CPK levels detected in the serum within 8 hours of the bite (Hyde and Driasey, 1974). The precise cause of the higher level of serum glucose are not determinable at this stage as heart failure, malfunction of the kidneys, thyroid, liver and pancreas cause glucose increase. Of these organs changes were seen histologically in the heart, kidneys and liver which may explain the increased glucose levels at an early stage.





- Fig. 8. Section of skin from the bite-site 6 hours after envenomation. The epidermis is completely lysed by this stage and overlies a collagen layer which is intensely haemorrhagic and necrotic. (H & E, 150 x).
- Fig. 9. Evidence of vasculitis 6 hours after the bite. The vessel (cut longitudinally) is partly occluded by fibrin thrombi clots and inflammatory cells. The collagen above the vessel is haemorrhaged and slightly oedematous. The muscle beneath the vessel is necrotic with karyolysis of the nuclei (H & E, 160 x).
- Fig. 10. Kidney showing necrosis at 6 hours after the bite but no evidence of haemoglobin casts. (H & E, 400 x).
- Fig. 11. An infiltrate of mononuclear cells and slight extravasation in between the striated muscle fibres of the endocardium. (H & E, 400 x).
- Fig. 12. Eosinophilic micro-abscess formation near portal vessels in the liver. (H & E, 400 x).
- Fig. 13. Pulmonary oedema, eosinophilic micro-abscess formation and widespread inflammatory cell infiltrates are clearly visible in this section of the lung, 6 hours after the bite (H & E, 160 x).

TABLE 1

Serum biochemistry results following *Sicarius albospinosus* bite in rabbits. The results reflect the pre-bite values (viz. normal) at time 0 and the findings at 4 and 8 hours after envenomation.

Time (hours)	Glucose	Alkaline phosphatase	ALT	AST	CPK	Amylase
0	7,2	43	79	25	343	506
4	9,9	85	156	144	496	456
8	16,1	292	760	1360	2018	436

ALT = alanine transaminase

AST = aspartate transaminase

CPK = creatinine phosphokinase

Paralysis of the hind limbs was thought to be due to a possible neurotoxic component in *Sicarius* venom. Neurotoxins which stimulate the adrenal, autonomic and sympathetic nervous systems generally give rise to very high levels of circulating catecholamines. High levels of catecholamines can induce cardiac arrest as is the case in scorpion envenomation but in the experiments I conducted, I got the impression that the rabbits died of respiratory failure rather than cardiac arrest. Catecholamine levels in a rabbit challenged with the venom of *Sicarius* was found to be greatly reduced prior to its death within eight hours of envenomation. The possible neurotoxic properties of *Sicarius* venom shall soon be studied in detail.

Besides the serum biochemical changes, discovered, numerous clinical tests revealed little or no abnormality, viz total protein, albumin, calcium, cholesterol, uric acid and bilirubin.

The haematological changes seen clearly suggest a DIC in my opinion. The diagnosis of DIC is confirmed by thrombocytopenia, depletion of fibrinogen, the activity of the clotting factors, accumulations of fibrin and fibrinogen degradation products (FDP) and prolonged prothrombin (PT) and partial thromboplastin (PTT) times (Bradlow, 1981). Rabbits subjected to the bite of *S. albospinosus* fulfilled all these requirements except increased levels of FDP (Table 2). The reason for this is not clear for in a single experiment conducted with the bite of *S. hahni*, the FDP levels in the blood rose dramatically within 6 hours of envenomation. This could be due to species specific differences in the action of the venom. An interesting feature of *Sicarius* envenomation was that clotting factor VIII is affected and drops to 16% of its activity within seven hours of the bite. When the activity of factor VIII drops below about 30%, systemic haemorrhaging is possible and this may account for the petechial haemorrhage seen in many of the visceral organs. Bradlow (1981) points out that factor VIII deactivation is rarely seen in DIC cases. Accordingly, the deactivation of factor VIII may be a unique feature of *Sicarius* envenomation. In my opinion the



DIC seen in the rabbits was a direct result of the effect on the clotting factor and not due to some secondary cause such as vasculitis or skeletal muscle damage.

TABLE 2

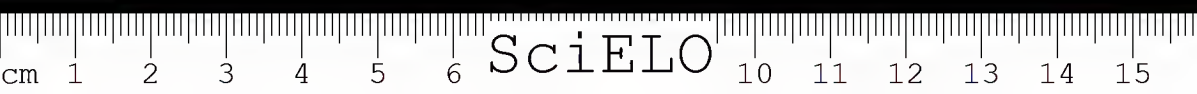
Clotting study on the blood of rabbits subjected to the bite of *Sicarius albospinosus*. Pre-bite values (viz. normal) are given at times 0 and the effect of the venom on the coagulation potential of the blood was assessed at various intervals after envenomation.

Time (hours)	PT (sec)	PTT (sec)	Fibrinogen (mg/dl)	FDP ($\mu\text{g}/\text{cm}^3$)	Factor VIII (% coagulent activity)
0	12,0	24,6	219	<10	100
1	—	—	199	10-40	75
2,5	—	—	210	<10	70
5	—	—	251	<10	38
6	—	—	139	<10	20
7,5	29,5	55,5	160	10-40	16

PT = prothrombin time
PTT = partial thromboplastin time
FDP = Fibrin degradation products

EPIDEMIOLOGICAL CONSIDERATIONS

Factors to be considered when assessing the medical importance of a highly venomous spider are those behavioural and distributional characteristics which regulate its potential contact with humans. The laboratory study of *Sicarius* envenomation in rabbits certainly suggests that *S. albospinosus* is one of the most dangerously venomous spiders in the world. The reasons for the low human accident levels with spiders of this genus in the past are of importance. In South Africa, I am aware of only two cases of spider envenomation which may have been caused by the bite of *S. spatulatus* (the smallest species in the genus) in the South eastern Cape. All southern African species of the genus except *S. spatulatus* occur in the sandy and extremely arid regions which are virtually uninhabited by humans (fig. 1). The microhabitat of these spiders further reduces the chances of human contact in that these spiders frequently bury themselves in the sand (as described by Reiskind 1965) beneath large rocks. Another habitat is beneath rocks in the twilight zone of caves or rock shelters. The spiders have a positive geotaxis and are never attached to the underside of their rock cover which greatly reduces the chances of accidents when field workers lift rocks. The spiders are very difficult to see when exposed because of their cryptic colouration and self burying behaviour and are thus unlikely to fall into the hands of most specimen collectors.



Besides the habitat choice, there are several unique behavioural attributes of *Sicarius* which greatly reduce their chances of human contact. In the laboratory, specimens of *Sicarius* would rarely of leave their shelter and rather than go out in search of food (as in the case of most spiders including *Loxosceles* species) these spiders would wait for the chance encounter of possible prey items wandering beneath their cover. The spiders bury themselves in the sand and then go into a state of diapause and often months go by before they move. Specimens kept in my laboratory refused food offered more frequently than every two or three months and happily survived up to a year without feeding. Nothing is known of their mating frequency in nature and whether males go in search of females or visa versa. I have only once seen specimens of *Sicarius* walking about in the field and this may have been caused by my disturbing their habitat while collecting arachnids in the vicinity. These spiders live a very long time. An adult female *S. albospinosus* I collected at Tsondab Vlei in the Namib during June 1970 died in October 1980 after it had been handled roughly in envenomation experiments. Another idiosyncrasy which reduces the medical importance of *Sicarius* species is the fact that they appear to bite with great reluctance. In all the laboratory tests, the spiders had to be pressed firmly into contact with the rabbit and in most cases, had to be provoked by pulling their pedipalps with fine forceps before they would bite.

On the negative side, because *Sicarius* specimens are normally in a state of diapause, they do not move when disturbed and could easily be mistaken for dead specimens. Anyone handling such a specimen could be bitten when the spider 'awakes'. Furthermore, one species, *S. spatulatus* occurs in the relatively densely populated areas of the south eastern Cape Province in South Africa and this species has possibly been involved in two human accidents in the East London area. In these cases, the spider was not identified but the description provided by one of the victims fit that of *S. spatulatus*. In this particular case the victim lost an arm because of the extensive tissue necrosis. Other areas where *Sicarius* species occur and which have relatively high human population densities are indicated in figure 1. Most of these high risk areas are in Central and South America, viz. El Salvador, Costa Rica, Colombia, Equador, Peru, Brazil and Argentina.

CONCLUSION

Laboratory studies have demonstrated that at least two South African species of *Sicarius* are dangerously venomous. Fortunately, the behaviour and ecological background of these species is such that the chances of human accidents in South Africa are slight. However, with the increasing human activities in the deserts of southern Africa, the chances of human involvement with these spiders increases yearly. While species specific toxicological differences were detected in some of the experiments, all species of the genus in southern Africa and the Americas should be regarded as dangerous until proved harmless. There are several areas in South and Central America where species of *Sicarius* occur in relatively



densely populated areas. In South Africa, the high risk areas are Cape Town and the Port Elizabeth-East London areas, where a small species, *S. spatulatus* occurs.

In South America bites of the spider *Loxosceles laeta* are frequently accompanied by serious systemic symptoms (Schenone, 1978), and it is possible that some of these cases diagnosed on signs and symptoms alone, could be confused with cases of *Sicarius* envenomation which is superficially similar.

While the names *S. albospinosus* and *S. hahnii* have been used, great difficulty was experienced in matching specimens with the type species descriptions. Gerschman de Pilken and Schiapelli (1979) encountered the same difficulty in their study of Argentinian species. In view of the fact that the various species I have studied are not equally toxic, a thorough taxonomic revision of the species is urgently required.

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NEW WORLD CORAL SNAKES (ELAPIDAE): A TAXONOMIC AND BIOLOGICAL SUMMARY

Janis A. ROZE *

Coral snakes (corales, coralillos, coralillas, cobras coraes) comprise a group of about 120 species and subspecies of elapid snakes of the New World. Presently, they are included in two genera, *Micruroides*, known from southeastern United States and western Mexico, and *Micrurus* distributed throughout the tropical and warm-temperate parts of North, Central and South America, from North Carolina, Florida, Arizona and Texas, United States to central Argentina. A third genus, *Leptomicrurus*, invalidated by Romano (1972), has some characteristics such as hemipenis structure, scale microornamentation (microdermatoglyphs), contact of the chin shields with the mental and the attachment of head musculature (attachment of the quarrate in rear of the venom gland) that suggest significant differences from the other species of the genus *Micrurus*. Additional information on venom characteristics, albumin as well as karyotypes might shed further light on this problem. Provisionally, the species of *Leptomicrurus* are included in the genus *Micrurus* pending further studies.

Over the last fifty years, the splitting as well as lumping tendencies have been evident in the taxonomy of coral snakes. The lumping, particularly occurring in the United States, is a recent Zeitgeist in herpetology. Maybe it has emerged as a reaction to the earlier splitting tendencies, or as a fascination for the potential of computer analysis applied to taxonomy and classification. On many occasions, the latter can neutralize biases and subjective interpretation of data and thus eliminate guesswork and speculations. At the same time, however, an excessive use of computer-generated "absolutes" transform and consequently restrict the elegant art of taxonomy and evolutionary assessment of species to a mathematical, mechanistic game, be it cladistic, chronistic or phenic. Fortunately, new knowledge in additional fields is becoming available which broaden the decision base and add new dimensions to taxonomic inquiries. Such fields as genetic karyotyping, serological and tissular analysis, comparative biochemistry and pharmacological properties of venoms, diversity and evolution of behavior, niche analysis and ecological partitioning of resources to name a few are creating the potential for a holistic definition and understanding of species, subspecies and even

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intersubspecific populations. This holistic species concept — strived for by many systematically and evolutionary oriented biologists — might be the most integrative approach by which a species or subspecies is defined.

In addition, two important ingredients of the taxonomist's work are field studies and ecological assessment of a species, especially useful when revising widely distributed taxonomic groups. As many seasoned biologists would testify, during intensive field research a "biological sense of a species or subspecies" is frequently developed. It facilitates not only an empirical perception of the species gestalt in its natural environment but might also serve as additional information to be translated later into quantitative and quantifiable terms. What I am suggesting here is a kind of "biologist's intuition", similar to what has been described of physicists. They might have an intuitional perception of a basic concept or a solution to a problem but these intuitions must be expressed in mathematical or logical terms. The integration of intellectual data with the intuitional perception, developed during field or laboratory studies, might be a framework for a holistic exercise in any field of biological endeavor.

Such complex coral snake species as *Micrurus diastema*, found in Mexico and northern Central America, and *Micrurus nigrocinctus*, from Central America to northwestern Colombia, are comprised of groups of subspecies and even population complexes that have been lumped together (Wilson and Mayer, 1972; Fraser, 1973; Savage and Vial, 1974) even though additional biological evidence suggests the validity of their subspecific subdivisions. Both species are, probably, of a relatively recent evolutionary origin that have undergone migrations and adaptive radiation that would fascinate an evolutionary biologist. Insular forms of *M. nigrocinctus*: *M. n. babaspul*, *M. n. coibensis* and *M. n. ruatanus* probably represent three different states of geographical formation of races and speciation. The rather distinct *M. n. ruatanus* has not only developed a distinct set of characteristics, close to species level of differentiation, but is presently endangered by human activities (Wilson and Hahn, 1973). Even a more dramatic situation is found with *M. n. babaspul*, an inhabitant of the Isla del Maíz Grande (Great Corn Island), Nicaragua. The Babaspul, as the natives of the island call it, has not only disappeared from the nearby Isla del Maíz Pequeña (Little Corn Island), but its distribution on the first island has been reduced to a small area not yet subject to human exploitation. If things go on as they do, in about 20 or 30 years another subspecies will be added to the growing list of extinct animals by action of humans.

From the present studies of coral snakes and other groups of vertebrates it is becoming increasingly obvious that a recognition and careful definition of taxonomic units particularly to the subspecific level is a contemporary taxonomic imperative. In many cases it is not an easy task. Yet, additional data from chromosome studies, venom characteristics, serological and ecological features and other studies facilitate a holistic definition of subspecies where they can be recognized. At the same time, a precise definition of species and subspecies is a contribution of systematic and evolutionary biology that provides a basis for a better assessment of differences and variation in ecological and evolutionary dynamics of the taxonomic units. It provides also a framework for



assessment of species and subspecies of medical and epidemiological importance. One such example is the excellent research of Oswaldo Vital Brazil (1980) in coral snake venoms for which the subspecific definition and distribution of the real life units (subspecies) could have helped in a more precise interpretation of the differences in venom characteristics of two closely allied species: *Micrurus frontalis* ssp. and *M. lemniscatus* ssp. from southern Brazil. The differences of venom characteristics (cf. protein contents and other characteristics) and level of aggressivity found between the two subspecies of coral snakes in the United States (*Micrurus fulvius fulvius* and *M. f. tenere*) is another example in which the recognition of subspecific differences becomes an important factor in interpreting these differences.

In continuation, some biological features of coral snakes are briefly summarized together with an updated enumeration of the recognized genera, species and subspecies.

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BIOLOGICAL SUMMARY

Food

Most coral snakes are foraging ground litter feeders. About 90% of the species are ophiophagous, including cannibalism, but about 60% have more euryphagous habits, feeding also on other elongated amphibians and reptiles. In addition to snakes, several subspecies of *M. frontalis*, *M. mipartitus semipartitus*, *M. eorallinus*, *M. lemniscatus* ssp. and *M. t. tschudii* feed also on amphisbaenids. Caecilians are known prey items for *M. latifaciatus*, *M. n. nigrocinctus*, *M. spixii obscurus* and *M. lemniscatus helleri*.

At least four species (*M. alleni*, *M. dumerilii carinicauda*, *M. lemniscatus duitius*, *M. lemniscatus helleri* and *M. s. surinamensis*) feed on a

tropical pound and swamp dwelling eel, *Synbranchus marmoratus*. Stomach content of *M. lemniscatus helleri* from Peru from specimens at the American Museum of Natural History and National Museum of Natural History suggest an ontogenetic dietary change. The smaller specimens feed on a snakelike teiid lizard, *Ophiognomon trinasale*, while the larger specimens of *M. l. helleri* feed on *Synbranchus*. *Micruroides e. euryxanthus* feeds predominantly on blind snakes (*Leptotyphlops humilis*) while *Micrurus narducci* (*Leptomicrourus auct.*) feeds on microteiid lizards.

One remarkable departure from the vertebrate diet is found in *M. hemprichi ortonii* that feeds exclusively on *Peripatus*, an onychophoran invertebrate related to arthropods (Stomach contents of several specimens from Ecuador (ANMH No. 28816) and Peru (AMNH Nos. 2793 and 53182, and Dixon and Soini, 1973). Another subspecies, *M. h. hemprichi* from Guyana feeds on lizards and snakes.

In captivity, many species accept prey other than their natural food, including frogs and pink mice and other species of reptiles.

The most complete inquiry into food/feeding of coral snakes was done by Greene (1974); additional data are found in Schmidt (1932), Beebe (1946), Vitt and Hulse (1973), and Dixon and Soini (1973).

Feeding

Coral snakes search for prey with random poking movements, crawling slowly in ground litter, leaves, sand or grass, depending upon the substrate of the habitat. It seems that some coral snakes can follow pheromonal trails left behind by the prey species in order to locate their hiding place. Tongue flicking is performed within the physical proximity of a prey or around objects that might constitute a prey.

Once a prey is located and properly identified, the coral snake would strike. Due to the limited vision of coral snakes biting intents are not always successful. When the prey has been bitten and seized, most coral snakes hang on to the prey and perform a chewing motion part of which serves to introduce more venom in the prey. A struggle ensues that usually ends with partial or total envenomation of the prey. A part of the struggle for overpowering the prey, while maintaining the bite grip, the coral snake might use a loop of its body to press down and dominate a lizard prey. Some species recur to the display of self-mimicry tail-raising "lure", apparently to distract a snake prey and divert it from biting the coral snake's body while the latter holds on to the prey, as I have observed it in feeding of *M. isozonus* from Venezuela.

Most coral snakes do not release the prey and perform preingestion maneuvers consisting of "jaw-walking" along the body toward the anterior end of the prey. Over 95% of the prey is ingested head first. Depending upon the nature of the prey, swallowing is performed quickly, usually from a few to ten minutes. The total feeding process, as observed in captivity, from encountering the prey to finishing the ingestion may last from a few minutes to several hours. After the first prey, the coral snake is ready to respond to the presence of a second prey.



Observations of feeding of *M. isozonus* in captivity and the presence of several freshly ingested prey items found in stomachs of *M. latifasciatus* and *M. diastema* apiatus indicate that coral snakes devour more than one prey item within a given feeding period.

Cannibalism

Interspecific and intraspecific cannibalism is a rather remarkable phenomenon among coral snakes. Since Amaral's (1933) general remarks about cannibalism in *M. ibiboboca*, several more species have been found to be cannibalistic: *Micrurus lemniscatus diutius* (Wehekind, 1955), *M. psyches circinalis*, *M. f. fulvius* and *M. fulvius tenere* (Loveridge, 1944; Greene, 1974). In *M. f. fulvius*, up to 12% of prey represent a low but persistent level of cannibalism.

There are no good explanations of cannibalism in coral snakes. Probably, the similarity in shape to the natural prey plays some role as well as weakly developed pheromonal communication system.

Interspecific predation is also known as determined from the stomach contents of museum specimens. A specimen of *M. spixii obscurus* had eaten a *M. a. annellatus* (in Naturhistorisches Museum, Vienna), and a *M. lemniscatus diutius* had eaten a *M. psyches circinalis* (Wehekind, 1955).

Defense behavior

Coral snake defense against predators or supposed predators has a diverse repertoire of interdependent morphological and behavioral patterns. These can be considered separately, but the actual presence of a predator will elicit a combination of effects of coloration and behavior in accordance to the best possible strategy for a successful encounter (survival). That is to say, aposematic coloration does not seem to be the principal mechanism of defense but forms part of a holistic behavioral gestalt created by coloration and behavior. Moreover, in certain situations the warning coloration might contribute to a mimicry system or even become a concealing and disruptive coloration in "blotched background" during rapid erratic movements by the coral snake (Greene and Pyburn, 1974).

The defense posture in many species of coral snakes includes self-mimicry or auto-mimicry. It consists of hiding the head beneath body coils, flattening the posterior part of the body, curling and raising the tail together with some part of the body with erratic sham-aggressive movements. Some species, such as *M. surinamensis nattereri* from Venezuela, flattens almost the entire body. The use of tail is enhanced by the brilliant coloration (Gehlbach, 1972) and apparently serves as an intimidating device more than a strategy of misdirecting the attack of the predator (Greene, 1973). Yet in captivity, *M. isozonus* was observed using its tail display to "lure" away the bite of a prey snake, while the coral snake was hanging on to the prey with a chewing motion.

M. mipartitus semipartitus and *M. fulvius* ssp. also employ a sporadic "striking with the tail" (Test *et al*, 1966; Gehlbach, 1970). *M. frontalis* ssp., in addition to "striking with the tail", displays a death-feigning

defense behavior. In some species (cf. *M. corallinus*) no self-mimicry has been observed; only some flattening of body.

A special defense behavior has been evolved by *Micruroides e. eurysanthus* consisting of a noise produced by cloacal popping performed during the attack of a predator or enemy (Bogert, 1960).

Mimicry

Coral snakes constitute a unique group among vertebrates that participate in mimicry systems as a model as well as a mimic encompassing a large number of species. In fact, the coral snake coloration mimicry systems seem to be the largest single functional mimicry color pattern in the animal kingdom. The complex mimicry interdependencies span the whole gamut of known mimicry interactions. Ranging from Batesian to Mullerian mimicry they involve non-venomous, mildly venomous and very venomous species. Greene and McDiarmid (1861) reviewed all the arguments for and against the phenomenon of coral snake mimicry. The extraordinary concordance of color patterns between *Micrurus* and species of several genera of colubrid snakes, at times in nearly 100% of the species and subspecies as in *Pliocereus*, suggests that mimicry is a significant factor in natural selection and evolution of the species.

Among the mildly venomous species are aglyphous (cf. *Pliocereus*) as well as opisthoglyphous (cf. *Erythrolamprus*) species. The non-venomous mimics include species from several general (cf. *Atractus*, *Lampropeitis*, *Anilius*). Such non-venomous species as *Atractus elaps* and *Atractus güntheri* in Amazon and Orinoco drainages mimic not only more than one species of coral snakes (*M. margaritiferus* and *M. l. langsdorffi*) but show a polymorphism of not mimicking any other species, a well known phenomenon among model-mimic species systems in butterflies. Moreover, *M. l. langsdorffi* itself is a polymorphic subspecies (Soini, 1974).

An intriguing question here is, can subspecies or even different species of these mimicking *Atractus* species or species complexes be recognized? This particular mimicry system is an illustration of mimicry systems of coral snakes with non-aposematic coloration.

Deviation from a predominant color pattern of a *Micrurus* species and its concordance with another sympatric *Micrurus* species indicates the existence of another type of Mullerian mimicry. In several cases when the distribution of a single banded species overlaps with a species of a triad type color pattern, the first tends to mimic the second. For example, *M. mertensi* in northern Peru is single banded but in the region of Loja, in southern Ecuador, where its distribution overlaps with that of *M. bocourti*, a species with accessory type triads, *M. mertensi* has developed a form with weak but clearly distinct accessory triad type pattern. Another example is *M. d. dumerilii* from lower Magdalena valley in northern Columbia. All subspecies of *M. dumerilii* except two are single banded forms. In lower Magdalena where it is sympatric with *M. dissoleucus nigrirostris*, a triad type form, the subspecies, *M. d. dumerilii* shows accessory triad type pattern. The same happens with *M. dumerilii*

colombianus in Santa Marta region where it is sympatric with *M. dissolcucus melanogenys*. However, at least one morph of *M. d. dumerilii* with nearly perfect single banded pattern has also been found within the area of distribution of *M. dissolcucus nigrirostris*. That the color patterns are not convergent in this type of Mullerian mimicry is demonstrated by the fact that the single banded pattern adopts the triad type pattern and not vice-versa. This would also suggest that the triad type color pattern is a more recent pattern developed from a single banded coloration and the triad type snake can not "go back" again to a single banded pattern, supporting the concept of evolutionary irreversibility of morphological characteristics.

Interspecific mimicry influences among species of *Micrurus* is suggested also by divergence of other, more general features of coloration within sympatric species. One example is the supracephalic coloration of *M. lemniscatus carvalhoi* in the area of distribution of *M. frontalis brasiliensis*. The clearly defined whit and red bands of the former become irregular approaching to the pattern found in *M. frontalis brasiliensis*. The irregularity of black bands and the presence of black tips on the white scales of *M. l. carvalhoi* is also suggestive of the coloration found in *M. f. brasiliensis*. Expanded red bands of *Micruroides euryxanthus australis* and *M. e. neglectus* in the area of distribution of *Micrurus d. distans*, a species with long red bands seems to indicate the same condition. Apparently, the mimicry system confers greater selective advantage than the phenomenon of divergence known in sympatric conditions where two quite similar species coexist.

In the Amazon basin most coral snake species have a tendency to melanism as found in *M. albieinctus*, *M. l. langsdorffi*, *M. putumayensis*, *M. margaritiferus* and several subspecies of *M. psyches*. One subspecies, *M. psyches circinalis* — outside the Amazon basin — distributed in Trinidad and northeastern Venezuela, has no melanistic tendencies, or very limited. Instead, many individuals have developed weak accessory black bands, approaching to *M. lemniscatus diutius*, a triad form found sympatric with *M. psyches circinalis*.

The mimefactors are predators, mostly birds but also mammals. The wide distribution of predator species can maintain a mimicry system even when the model-mimic assemblages are not sympatric but occupy adjacent areas or different habitats within the general area of distribution.

Whereas in North and Central America coral snakes are either alone or are sympatric usually with only one more species, in South America, especially in the Amazon basin, up to eight species are known to coexist. They display very complex patterns of partition of resources and niche differences several of which are still only partially known (Henderson, Dixon and Soini, 1979). A considerable niche overlap exists as well as other convergencies without clearly convergent mimicry systems, apart from the general color patterns. In such sympatric assemblages some habitat segregation exists as for example between *M. l. langsdorffi* and *M. putumayensis*. Adding to this coral snake group the nine non-elapid mimics found in the same region around Iquitos, Peru results in a complex mimicry assemblage of at least 17 species.

Karyotypes

The number of chromosomes (2n) of the six species and subspecies of coral snakes studied thus far ranges from 26 to 42. The first chromosomal study of a coral snake, *Micrurus lemniscatus carvalhoi*, from Brazil was done by Beçak and Beçak (1969) who found for this subspecies a total of 42 chromosomes (22 macrochromosomes and 20 microchromosomes). Recently, active karyotype research has been done by Gutiérrez and Bolaños (1979, 1981) on Costa Rican species. *M. n. nigrocinctus* has 26 (16 + 10), *M. n. mosquitensis*, 30 (16 + 14), *M. alleni*, 34 (20 + 14), while *M. multifasciatus hertwigi* has 34 (14 + 20) chromosomes. The Texas Coral Snake, *M. fulvius tenere*, has 32 (16 + 16) chromosomes (Graham, 1977).

Coral snakes have ZZ-ZW pattern of sex chromosomes, homologous for males and heterologous for females. This pattern has been also found in several Old World elapids.

Significant intersubspecific differences are found in the subspecies of *M. nigrocinctus* from Costa Rica, conforming the subspecific validity of *M. n. nigrocinctus* and *M. n. mosquitensis*. At the same time, Gutiérrez and Bolaños (1981) reported interesting chromosomal polymorphism in *M. n. nigrocinctus*.

TAXONOMIC SYMMARY

Taxonomic novelties

The following is a list of taxonomic changes since the check lists by Roze (1967 and 1970). Reasons for the proposed changes appear in the general check list under each taxonomic unit. A new subspecies of *Micrurus frontalis* is described from Bolivia.

<i>Taxonomic unit</i>	<i>Present allocation and status</i>
<i>Micrurus alleni yatesi</i> DUNN, 1942	<i>Micrurus alleni</i> SCHMIDT, 1936
<i>Micrurus annellatus montanus</i> SCHMIDT, 1954	<i>Micrurus annellatus annellatus</i> , (PETERS), 1871
<i>Micrurus bocourti bocourti</i> (JAN), 1872	<i>Micrurus bocourti</i> (JAN), 1872
<i>Micrurus bocourti sangilensis</i> NICEFORO MARIA, 1942	<i>Micrurus sangilensis</i> NICEFORO MARIA, 1942
<i>Micrurus donosoi</i> HOGE, CORDEIRO and ROMANO, 1976	<i>Micrurus psyches donosoi</i> HOGE, CORDEIRO and ROMANO, 1976
<i>Micrurus fitzingeri</i> (JAN), 1858	<i>Micrurus fulvius fitzingeri</i> (JAN), 1858
<i>Micrurus frontalis mesopotamicus</i> BARRIO and MIRANDA, 1968	<i>Micrurus frontalis baliocoryphus</i> (COPE), 1859

<i>Micrurus lemniscatus multicinctus</i> AMARAL, 1944	<i>Micrurus frontalis multicinctus</i> AMARAL, 1944
<i>Micrurus tricolor</i> HOGE, 1956	<i>Micrurus frontalis tricolor</i> HOGE, 1956
<i>Micrurus lemniscatus frontifascia-</i> <i>tus</i> (WERNER), 1927	<i>Micrurus frontifasciatus</i> (WER- NER), 1927
<i>Micrurus mipartitus hertwigi</i> (WERNER), 1897	<i>Micrurus multifasciatus hertwigi</i> (WERNER), 1897
<i>Micrurus mipartitus multifasciatus</i> (JAN), 1858	<i>Micrurus multifasciatus multifas-</i> <i>ciatus</i> (JAN), 1858
<i>Micrurus nigrocinctus melanoce-</i> <i>phalus</i> (HALLOWELL), 1855	<i>Micrurus nigrocinctus nigrocinct</i> (HALLOWELL), 1855
<i>Micrurus nuchalis</i> SCHMIDT, 1933	<i>Micrurus latifasciatus</i> SCHMIDT, 1933
<i>Micrurus ruatanus</i> (GUNTHER), 1859	<i>Micrurus nigrocinctus ruatanus</i> (GUNTHER), 1859
<i>Micrurus steindachneri petersi</i> ROZE, 1967	<i>Micrurus petersi</i> ROZE, 1967
<i>Leptomicrourus</i> species	Provisionally included in <i>Micrurus</i> .

Check list of species and subspecies

Genus MICRUROIDES

Micruroides euryxanthus euryxanthus (Kennicott)

Elaps euryxanthus Kennicott, 1860, Proc. Acad. Nat. Sci. Philadelphia, 12:337. (Type locality: Sonora, Mexico).

Distribution: Southern Arizona and southwestern New Mexico, United States to northern Chihuahua and Sonora, Mexico.

Micruroides euryxanthus australis Zweifel and Norris

Micruroides euryxanthus australis Zweifel and Norris, 1955, Amer. Midland Nat., 54(1):246. (Type locality: Guirocoba, Sonora, Mexico).

Distribution: Southern Sonora and probably Chihuahua, Mexico.

Micruroides euryxanthus neglectus Roze

Micruroides euryxanthus neglectus Roze, 1967, Amer. Mus. Novitates, 2287:4, fig. 1. (Type locality: Sixteen and three-tenths miles north-northwest of Mazatlán, Sinaloa, Mexico).

Distribution: Vicinity of Mazatlán, Sinaloa, Mexico.

Genus MICRURUS

Micrurus albicinctus Amaral

Micrurus albicinctus Amaral, 1926, *Comm. Linh. Telegr. Mato Grosso*, Publ. 84, Annex 5:26, figs. 7-10. (Type locality: No specific type locality given; collection containing the specimen came from "Northern or central Mato Grosso, Brazil").

Micrurus wachnerorum Meise, 1938, *Zool. Anz.*, 123(1/2):20. (Type locality: São Paulo de Olivença, Brazil).

Distribution: From middle Amazon to Mato Grosso, Brazil.

Micrurus alleni Schmidt

Micrurus nigrocinctus alleni Schmidt, 1936, *Zool. Ser. Field Mus. Nat. Hist.*, 20:209, fig. 25. (Type locality: Río Mico, seven miles above Rama, Siquiá District, Nicaragua).

Micrurus nigrocinctus yatesi Dunn, 1942, *Notulae Naturae*, 108:8. (Type locality: Farm Two, Chiriquí Land Co., near Puerto Armuelles, Chiriquí, Panama).

Micrurus alleni richardi Taylor, 1951, *Univ. Kansas Sci. Bull.*, 34:169, pl. 23, fig. (Type locality: Los Diamantes, 2 km south of Guápiles, Costa Rica).

Distribution: From eastern Nicaragua, Costa Rica to western Panama.

Notes: Apparently, this species is represented by two disconnected populations. One is found on the Atlantic side and the other on the Pacific side of southern Central America. The specimens from the Atlantic side have predominantly white bands while the Pacific specimens have yellowish bands that are particularly intense in individuals from southeastern part of Costa Rica. Yet, some individuals from Bocas del Toro lowlands in western Panama have yellow bands as well. Most specimens of the population from the Pacific lowlands of southeastern Costa Rica and adjacent Panama as well as from the drier low montane forests of Boquete and Volcán Chiriquí have the red bands nearly completely obliterated by black.

As noted by Savage and Vial (1974) other characteristics such as the number of ventrals and subcaudals and of body bands overlap in their extreme values. Consequently, it is difficult to separate *M. alleni yatesi* as a distinct subspecies, until more specimens are available.

Micrurus ancoralis ancoralis (Jan)

Elaps maregravii var. *ancoralis* Jan, 1872, in Jan and Sordelli, *Icon. Gen. Ophid.*, Liv. 42: pl. 4, fig. 2. (Type locality: Ecuador).

Elaps rosenbergi Boulenger, 1898, *Proc. Zool. Soc. London*, 1898:117, pl. 13. (Type locality: Paramba, Esmeraldas Province, Ecuador).

Distribution: Northwestern Ecuador.

Micrurus ancoralis jani Schmidt

Micrurus ancoralis jani Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., 20:197. (Type locality: Andagoya, Chocó, Colombia).

Distribution: Eastern Panama to Chocó region of western Colombia.

Notes: Both subspecies intergrade in the Saija drainage, Cauca, Colombia.

Micrurus annellatus annellatus (Peters)

Elaps annellatus Peters, 1871, Monatsber. Akad. Wiss. Berlin, 1871:402. (Type locality: Pozuzo, Peru).

Micrurus annellatus montanus Schmidt, 1954, Fieldiana: Zool., 34:322. (Type locality: Camp Four, about ten km north of Santo Domingo Mine, Puno, Peru, 2000 m).

Distribution: Amazonian slopes of Andes in southern Ecuador, Peru to central Bolivia.

Notes: Additional specimens from Peru show a variation in the length of the light parietal and presence or absence of the red bands seems to be at least partially related to ontogenetic growth. Both of these characteristics were used by Schmidt (1954) to describe *M. annellatus montanus*.

Specimens from higher altitudes exhibit tendency to have a wider parietal white band and the red bands are darker but still distinguishable. Black-white specimens, however, are also present (5 out of 15). Some of them have a very narrow white parietal band that occupies barely one eighth to one quarter the length of the parietals. Of the two specimens from the same locality, Hacienda Cadena, Marcapata Valley, Cuzco, Peru, one has the characteristics of *M. a. annellatus* (FMNH No. 62942) and the other those of *M. a. montanus* (FMNH No. 40223). The first is a black-white specimen (with a body length of 413 mm) with the white parietal band about one quarter the length of the parietals, whereas the second is a black-red-white specimen (with a body length of about 195 mm) with the white parietal band about two thirds the length of the parietals.

All specimens from the Peruvian Amazon, up to 1000 m above sea level are black-white. Between 1000 m and 2000 m of altitude both black-white and black-red-white specimens are known even though specimens of the latter coloration comprise 80%. Two specimens from Beni Province, Bolivia (AMNH Nos. 2975-6) are black-white. Consequently, *M. a. montanus* must be regarded as a synonym of the nominal subspecies. This disposition might be modified when more specimens and their altitudinal data are available.

Micrurus annellatus balzani (Boulenger)

Elaps balzani Boulenger, 1899, Ann. Mus. Stor. Nat. Genova, (2)19:130. (Type locality: Yungas, Bolivia).

Elaps regularis Boulenger, 1902, Ann. Mag. Nat. Hist. (7)10:402. (Type locality: Chulumani, Bolivia, 2000 m).

Distribution: Western Bolivia.

Notes: No melansitic tendencies or obliteration of the red bands by black is known in this subspecies. ZMH No. 5396 from San Carlos, Beni, Bolivia can be considered intergrade between this and the nominal subspecies.

Micrurus annellatus bolivianus Roze

Micrurus annellatus bolivianus Roze, 1967, *Amer. Mus. Novitates*, 2287: 7, fig. 2. (Type locality: Rio Charobamba, about 50 km northeast of Zudanez, Chuquisaca, Bolivia).

Distribution: Eastern Andes and high Amazon Valleys in Cochabamba and Chuquisaca, central Bolivia.

Micrurus averyi Schmidt

Micrurus averyi Schmidt, 1939, *Zool. Ser. Field Mus. Nat. Hist.*, 24:45, fig. 5. (Type locality: At head of Itabu Creek, Courantyne District, British Guiana (= Guyana) 2000 ft., near Brazilian border, at Lat. 1°40'N and Long. 58°W).

Distribution: Southern tip of Guyana to Manaus, Amazonas, Brazil.

Notes: Three additional specimens from Reserva Duke, near Manaus, Amazonia, Brazil in the Instituto Butantan (IB Nos. 32492, 43194-5) are the only specimens known in addition to the holotype. They extend the distribution of this species into Brazil. This species might be related to *M. psyches* by the absence of supraanal tubercles and by the all black head coloration.

Micrurus bernardi (Cope)

Elaps bernardi Cope, 1887, *Bull. U. S. Natl. Mus.*, 32:87. (Type locality: Zacualtipan, Hidalgo, Mexico).

Distribution: Western Hidalgo and northern Puebla, Mexico.

Notes: In this species the black bands are reduced to black dorsal spots.

Micrurus bocourti (Jan)

Elaps Bocourti Jan, 1872, in Jan and Sordelli, *Icon. Gén. Ophid.*, Liv. 42, pl. 6, fig. 2. (Type locality: Unknown, restricted to Rio Daule, Provincia de Guayas, Ecuador by Roze, 1967).

Micrurus ecuadorianus Schmidt, 1936, *Zool. Ser. Field Mus. Nat. Hist.*, 20:196. (Type locality: Rio Daule, western Ecuador).

Distribution: Western Ecuador and northern Peru.

Notes: Apparently, the similarity between *M. bocourti* and *M. sangilensis* is purely superficial. Both forms have developed accessory black bands forming poorly marked black triads. About 1000 km separate the distribution of both species and no forms have been found inbetween. Therefore, *M. bocourti* is considered as a species unrelated to *M. sangilensis*.

In describing *M. ecuadorianus*, Schmidt (1936), apparently overlooked Jan's *E. bocourti* partially due to the complex history of its type specimen. Jan selected as type specimen for his *Elaps bocourti* one of the four specimens (= syntypes) that Duméril, Bibron and Duméril (1854) used in describing *Elaps circinalis* (= *M. psyches circinalis*). Three of them are presently registered in the Museum National d'Histoire Naturelle, Paris (MHNP Nos. 3912, 3913 and 869). MHNP No. 869 was selected by Jan (1872) as the type specimen for *Elaps bocourti*, and was illustrated in Jan and Sordelli's *Iconographie Générale des Ophidiens* in 1872. The specimen has 194 ventrals and 50 subcaudals and 2/3 17+7 black triads. It is a male specimen without supraanal tubercles. Roux-Esteve (1982) reviewed all the type specimens of coral snakes in the Paris Museum.

Micrurus bogerti Roze

Micrurus bogerti Roze, 1967, *Amer. Mus. Novitates*, 2287:9, fig. 3. (Type locality: Tangola-Tangola (Tangolunda), east of Puerto Angel, Oaxaca, Mexico.)

Distribution: Coastal belt between Puerto Angel and Tapanatepec, Oaxaca, Mexico.

Micrurus browni browni Schmidt and Smith

Micrurus browni Schmidt and Smith, 1943, *Zool. Ser. Field Mus. Nat. Hist.*, 29:29. (Type locality: Chilpancingo, Guerrero, Mexico.)

Distribution: Mexico City, state of Mexico and Sierra Madre del Sur from Guerrero southward to mountains of western Guatemala.

Micrurus browni importunus Roze

Micrurus browni importunus Roze, 1967, *Amer. Mus. Novitates*, 2287:11, fig. 4. (Type locality: Dueñas, about 25 kilometers west-southwest of Guatemala City in the Antigua Basin, Sacatepequez, Guatemala.)

Distribution: Known only from type locality.

Micrurus browni taylori Schmidt and Smith

Micrurus nuchalis taylori Schmidt and Smith, 1943, *Zool. Ser. Field Mus. Nat. Hist.*, 29(2):30. (Type locality: Acapulco, Guerrero, Mexico.)

Distribution: Region of Acapulco, Guerrero, Mexico.

Notes: This subspecies was known only from its holotype until Casas-Andreu and Lopez-Forment (1978) described 34 additional specimens from La Poza, Municipio de Acapulco, Guerrero, Mexico, found in composte piles of leaves in a nursery at the sea level.

Micrurus clarki Schmidt

Micrurus clarki Schmidt, 1936, *Zool. Ser. Field Mus. Nat. Hist.*, 20:211. (Type locality: Yavisa, Darién, Panama.)

Distribution: Eastern Costa Rica to western Panama.



Micrurus collaris (Schlegel)

Elaps collaris Schlegel, 1837, *Ess. phys. serp.* (1):448. (Type locality: Not given).

Distribution: Southeastern Venezuela, Guyana and adjacent Brazil.

Notes: Romano (1972) included this and other species of the genus *Leptomicrurus* in the genus *Micrurus*.

Micrurus corallinus (Merrem)

Elaps corallinus Merrem, 1820, *Tent. Syst. Amphiborum*: 144. (Type locality: Brazil, restricted to Rio de Janeiro, Cabo Frio, Brazil by Roze, 1967).

Distribution: Central and southern Brazil, south of the Amazon basin, and northern Argentina; probably also Uruguay.

Notes: The locality restriction (Roze, 1967) was based on the actual locality given by Wied (1820) for several specimens he collected and sent to Merrem for studies. The lectotype, designated by Roze (1966), is AMNH N.º 3911. It forms part of a larger collection purchased by the American Museum of Natural History, New York, around 1860.

Micrurus decoratus (Jan)

Elaps decoratus Jan, 1858, *Rev. Mag. Zool.*, (2)10:525, pl.B. (Type locality: Mexico (in error). Restricted to Serra da Bocaina, São Paulo, Brazil by Hoge and Romano, 1972).

Elaps fischeri Amaral, 1921, *Anex. Mem. Inst. Butantan*, 1:59, pl.2, figs. 1-5. (Type locality: Fazenda Bonito, Serra Bocaina, São Paulo, Brazil).

Elaps ezequieli Lutz and Mello, 1923, *Folha Médica*, 4:2 (Type locality: Caxambu, Serra da Mantiqueira, Minas Gerais, Brazil).

Distribution: Eastern and southeastern Brazil from Rio de Janeiro to Santa Catarina and Rio Grande do Sul.

Micrurus diastema diastema (Dumeril, Bibron and Dumeril)

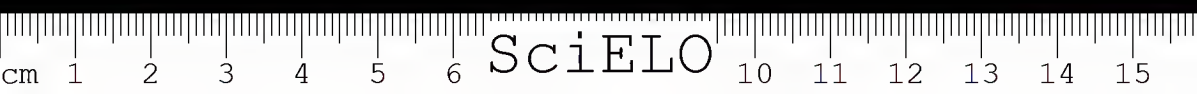
Elaps diastema Dumeril, Bibron and Dumeril, 1854, *Erp. Gen.*, 7:1222. (Type locality: Mexico, restricted to Colima, Mexico by Schmidt (1933). As this locality is far outside the range of this subspecies, it is not valid. Restricted herewith to Potrero Viejo, Veracruz, Mexico. See notes.)

Elaps epistema Duméril, Bibron and Duméril, 1854, *Erp. Gén.* 7:1222. (Type locality: Mexico).

Elaps corallinus var. *crebipunctatus* Peters, 1869, *Montasber. Akad. Wiss. Berlin*, 1869:877. (Type locality: Matamoras, Puebla, Mexico).

Distribution: Central Veracruz and eastern Puebla, Mexico.

Notes: *M. diastema* represents one of the most complex *rassenkreis* of coral snakes. Its distribution as well as its morphological variation shows intricate patterns of variation, cline formation and specialization. Fraser (1973) made a thorough analysis of its geographical variation concluding that no subspecies can be recognized. Yet, once the zones of inter-



gradation are identified and the intergrades, showing intermediate features of intergradation excluded from the analysis, a set of clearly defined subspecies can be recognized with non-overlapping characteristics. The subspecific validity of *M. diastema alienus* as well as its intergradation, for example, has been confirmed by Blaney and Blaney (1979). Additional specimens and data of distribution from La Gloria, Oaxaca (UI Nos. 35629-32, 37320-2) confirm the validity of another subspecies, *M. diastema macdougalli*.

M. distema is a complex rassenkreis of seemingly relatively recent evolutionary origin. It is undergoing formation of geographic races, adaptation and specialization to diverse ecological environments (cf. *M. d. alienus* to semixerix Yucatán Peninsula and *M. d. distema* to lowland and low montane wet forest in central Veracruz) in which broad zones of intergradation are still present (cf. between *M. d. diastema* and *M. d. sapperi* in eastern Veracruz and Tabasco, and between *M. d. alienus* and *M. d. sapperi* in Campeche and Quintana Roo, Mexico). Cline formation, as indicated by Fraser's excellent analysis, is also present in zones *M. d. sapperi* in Campeche and Quintana Roo, Mexico). Cline formation, as indicated by Fraser's excellent analysis, is also present in zones between two subspecies. The Cuautotolapan region in Veracruz might be even a region where three subspecies interbreed: *M. d. distema*, *M. d. sapperi* and *M. d. affinis*.

Micrurus diastema affinis (Jan)

Elaps affinis Jan, 1858, Rev. Mag. Zool., (2)10: 525. (Type locality: Mexico).

Distributions: Northern Oaxaca, Mexico.

Notes: This subspecies intergrades with *M. d. macdougalli* in northeastern Oaxaca in Ocatál, Buena Vista (UIMNH No. 37330).

Micrurus diastema aglaeope (Cope)

Elaps aglaeope Cope, 1860, Proc. Acad. Nat. Sci. Philadelphia, 1859:344. (Type locality: Honduras).

Distribution: Mountains of northwestern Honduras.

Micrurus diastema alienus (Werner)

Elaps alicnus Werner, 1903, Zool. Anz., 26:249. (Type locality: "Venezuela or Ecuador", restricted to Chichén Itzá, Yucatán, Mexico by Roze (1967)).

Micrurus affinis mayensis Schmidt, 1933, Zool. Ser. Field Mus. Nat. Hist., 20:37. (Type locality: Chichén Itzá, Yucatán, Mexico).

Distribution: Yucatán Peninsula: in Yucatán and northeastern Quintana Roo, Mexico.

Micrurus diastema apiatus (Jan)

Elaps apiatus Jan, 1858, Rev. Mag. Zool., (2)10:522. (Type locality: Veracruz, Mexico, shown to be a *lapsus* for Verapaz, Guatemala by Schmidt, (1933), and restricted to Cobán, Guatemala by Smith and Taylor (1950).

Distribution: Atlantic slopes of Alta Verapaz and Huehuetenango, Guatemala; probably also in eastern Chiapas, Mexico.

Notes: It intergrades with *M. d. sapperi* in the lowlands of Petén, Guatemala and in eastern Chiapas, Mexico. It intergrades also with *M. d. algaeops* in the area of low hills at the southwestern end of Lake Izabál, Guatemala.

Micrurus diastema macdougalli Roze

Micrurus diastema macdougalli Roze, 1967, *Amer. Mus. Novitates*, 2287:15, fig. 5. (Type locality: El Modelo, Rio Chalchijapa and Rio Corte, Oaxaca, Mexico).

Distribution: Atlantic slopes of Sierra Madre del Sur in eastern Oaxaca, Mexico.

Micrurus diastema sapperi (Werner)

Elaps fulvius var. *sapperi* Werner, 1903, *Abhandl. Bayerisch Akad. Wiss.*, 22(2):350. (Type locality: Guatemala).

Elaps guatemalensis Ahl, 1927, *Zool. Anz.*, 70(9/10): 251. (Type locality: Guatemala).

Micrurus affinis stantoni Schmidt, 1933, *Zool. Ser. Field Mus. Nat. Hist.*, 20:36. (Type locality: Belize, British Honduras (=Berlize)).

Distribution: Campeche, northern Chiapas and, probably, eastern Tabasco, Mexico to northern Guatemala and Belize.

Micrurus dissolencus dissolencus (Cope)

Elaps dissolencus Cope, 1860, *Proc. Acad. Nat. Sci. Philadelphia*, 1859: 345. (Type locality: Venezuela, restricted to Maracaibo, Zulia, Venezuela by Roze (1955)).

Distribution: Northeastern Colombia to eastern Venezuela.

Micrurus dissolencus dunni Barbour

Micrurus dunni Barbour, 1923, *Occ. Pap. Mus. Zool. Univ. Michigan*, 129:15. (Type locality: Ancon, Panama Canal Zone, Panama).

Distribution: Canal Zone to eastern Panama.

Micrurus dissolencus melanogenys (Cope)

Elaps melanogenys Cope, 1860, *Proc. Acad. Nat. Sci. Philadelphia*, 1860: 72. (Type locality: Unknown, restricted to Santa Marta region, Colombia by Schmidt, (1955)).

Elaps hollandi Griffin, 1916, *Mem. Carnegie Mus.*, 7:218, pl. 28, figs. 10-12. (Type locality: Bonda, Columbia).

Distribution: Santa Marta region, Colombia.

Micrurus dissolencus nigrirostris Schmidt

? *Elaps gravenhorsti* Jan, 1858, *Rev. Mag. Zool.* (2)10:522. (Type locality: Brazil).

Micrurus dissoleucus nigrirostris Schmidt, 1955, *Fieldiana, Zool.*, 34:355.
(Type locality: Barranquilla, Colombia).

Distribution: Lower Magdalena region, northern Colombia.

Notes: *Elaps gravenhorsti* Jan (1858) might represent this subspecies. However, the type specimen has been lost and its identity has never been established. In light of this uncertainty, I prefer to use the well defined *M. d. nigrirostris* Schmidt (1955).

Micrurus distans distans (Kennicott)

Elaps distans Kennicott, 1860, *Proc. Acad. Nat. Sci. Philadelphia*, 12:338.
(Type locality: Batosegachie (=Batosegachic), Chihuahua, Mexico).

Distribution: Southwestern Chihuahua and southern Sonora to Sinaloa and northwestern Nayarit, Mexico.

Notes: It intergrades with *M. d. zweifeli* in central Nayarit, Mexico.

Micrurus distans michoacanensis (Dugès)

Elaps diastema var. *michoacanensis* Dugès, 1891, *La Naturelleza*, (1)2:487, pl. 32. (Type locality: Michoacán, Mexico).

Distribution: Rio Balsas basin in Michoacán and Guerrero, Mexico.

Micrurus distans oliveri Roze

Micrurus distans oliveri Roze, 1967, *Amer. Mus. Novitates*, 2287:18, fig. 6.
(Type locality: Periquillo, Colima, Mexico).

Distribution: Colima, Mexico.

Micrurus distans oliveri Roze

Micrurus distans zweifeli Roze, 1967, *Amer. Mus. Novitates*, 2287:21, fig. 7. (Type locality: Laguna Santa María, Nayarit, Mexico).

Distribution: Southern Nayarit and Jalisco, Mexico.

Micrurus dumerilii dumerilii (Jan)

Elaps dumerilii Jan, 1858, *Rev. Mag. Zool.*, (2)10:522. (Type locality: Cartagena, Colombia).

Distribution: Lower Magdalena river region to Norte de Santander, Colombia.

Notes: *M. dumerilii* contains subspecies with single black banded pattern (*antioquiensis*, *carinicauda* and *transandinus*) and accessory triad type pattern (*dumerilii* and *colombiensis*). It suggests the process of development of triad type pattern from single banded pattern. Present subspecific arrangement is provisional until more specimens are available from some critical geographical areas in Colombia.

I thank Paulo Vanzolini for calling my attention to the correct use of this name (See Roze, 1970).

Micrurus dumerilii antioquiensis Schmidt

Micrurus antioquiensis Schmidt, 1936, *Zool. Ser. Field Mus. Nat. Hist.*, 20:195. (Type locality: Santa Rita, north of Medellín, Antioquia, Colombia).

Distribution: Cauca Valley, Colombia.

Micrurus dumerilii carinicauda Schmidt

Micrurus carinicauda Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., 20:194. (Type locality: Orope, Zulia, Venezuela).

Distribution: Northern Venezuela to Norte de Santander, Colombia.

Micrurus dumerilii colombianus (Griffin)

Elaps colombianus Griffin, 1916, Mem. Carnegie Mus., 7:216. (Type locality: Minca, Colombia).

Distribution: Santa Marta region of northern Colombia.

Micrurus dumerilii transandinus Schmidt

Micrurus transandinus Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., 20:195. (Type locality: Andagoya, Chocó, Colombia).

Distribution: Pacific lowlands of Columbia and northwestern Ecuador.

Micrurus elegans elegans (Jan)

Elaps elegans Jan, 1858, Rev. Mag. Zool., (2)10:524. (Type locality: Mexico, restricted to Jalapa, Veracruz, Mexico by Smith and Taylor, 1950).

Distribution: Central Veracruz and eastern Oaxaca to western Tabasco, Mexico).

Micrurus elegans veraepacis Schmidt

Micrurus elegans verae-pacis Schmidt, 1933, Zool. Ser. Field Mus. Nat. Hist., 20:32. (Type locality: Campur, Alta Verapaz, Guatemala).

Distribution: Chiapas and southern Tabasco, Mexico to Alta Verapaz, Guatemala.

Micrurus ephippifer (Cope)

Elaps ephippifer Cope, 1886, Proc. Amer. Philos. Soc., 23:281. (Type locality: Pacific side of the Isthmus of Tehuantepec (Oaxaca, Mexico)).

Distribution: Sierra Madre del Sur in Oaxaca to the Isthmus of Tehuantepec, Mexico.

Notes: The populations of higher altitudes of Sierra Madre del Sur show a considerable variation that might represent taxonomically distinguishable subspecies.

Micrurus filiformis filiformis (Gunther)

Elaps filiformis Gunther, 1859, Proc. Zool. Soc. London, 1959:86, pl. 18, fig. b. (Type locality: Pará, Brazil).

Distribution: Pará, along Amazon river to Manaus, Amazonia, Brazil.

Micrurus filiformis subtilis Roze

Micrurus filiformis subtilis Roze, 1967, Amer. Mus. Novitates, 2287:22, fig. 8. (Type locality: Caruru, Río Vaupes, Colombia-Brazil boundary).

Distribution: Upper Amazon region in northeastern Brazil, southern and southeastern Colombia to northeastern Peru.

Notes: It intergrades with the nominal subspecies around Carvoeiro, Amazonas, Brazil.

Micrurus frontalis frontalis (Duméril, Bibron and Duméril)

Elaps frontalis Duméril, Bibron and Duméril, 1854, *Erp. Gén.*, 7:1223. (Type locality: Corrientes and Misiones, Argentina (probably error)).

Distribution: Minas Gerais and northern São Paulo, westward to southern Mato Grosso and southern Paraguay.

Notes: *M. frontalis* is the most complex species in southern South America whose geographic variation has not yet been fully understood. Further material might reveal new arrangements of subspecies. Wide areas of intergradation and local geographic variations are known that further complicate the picture.

Micrurus frontalis altirostris (Cope)

Elaps altirostris Cope, 1860, *Proc. Acad. Nat. Sci. Philadelphia*, 1859: 345. (Type locality: South America).

Elaps heterochilus Mocquard, 1887, *Bull. Soc. Philom. Paris*, 7(11):39. (Type locality: Brazil).

Distribution: Southern Brazil in Rio Grande do Sul, and Uruguay; probably in northeastern Argentina.

Notes: The type specimen of *Elaps heterochilus*, a male from "Brazil" is probably an intergrade between *M. f. altirostris* and *M. f. multicinctus*. However, it has 29 subcaudals that is higher than in either subspecies. It also has the white bands slightly larger than the black bands, a condition not found in either subspecies. Another alternative is that the specimen is an intergrade between *M. f. baliocoryphus* and *M. f. altirostris* and comes from southeastern Brazil. The number of ventrals (209) of the type specimen is closer to *M. f. altirostris* (194-206 ventrals in males) than to any other subspecies. In light of its unusual characteristics not clearly assignable to any of the recognized subspecies, I prefer to consider it synonymous with *M. f. altirostris* with which it shares the red parietal coloration and the number of black triads (12).

M. f. altirostris intergrades with *M. f. multicinctus* in central Rio Grande do Sul and, probably, in northeastern tip of Argentina.

Micrurus frontalis baliocoryphus (Cope)

Elaps baliocoryphus Cope, 1859, *Proc. Acad. Nat. Sci. Philadelphia*, 1859: 346. (Type locality: Buenos Aires (in error), corrected and restricted herewith to Villa Federal, Entre Rios, Argentina).

Micrurus frontalis mesopotamicus Barrio and Miranda, 1968, *Mem. Inst. Butantan*, 33(1966):872, figs. 6-7. (Type locality: Villa Federal, Rios, Argentina).

Distribution: Provinces of Entre Rios, Corrientes and southwestern Misiones, Argentina.

Notes: The type specimen of *Elaps baliocoryphus* (ANSP No. 6842) undoubtedly represents this subspecies. It was considered a synonym of *M. f. frontalis*, but analysis of the Argentinian population of *M. frontalis* by Barrio and Miranda (1968) revealed the validity of this subspecies. Apparently, the type locality of Buenos Aires is an error and the type specimen has come to the United States from Argentina via Buenos Aires. *M. f. baliocoryphus* is distributed in the geographically well defined mesopotamic region of Argentina, between Rio Paraná and Rio Uruguay. Thus, Buenos Aires lies outside the geographic region in which *M. f. baliocoryphus* is known. The nearest locality where the subspecies is found is about 200 km north of the Argentinian capital.

In order to provide a realistic type locality for this well-defined subspecies, I propose a correction and restriction of the type locality to Villa Federal, Entre Rios, Argentina that was given as type locality for *M. f. mesopotamicus*.

M. f. baliocoryphus intergrades with *M. f. altirostris* north in the Misiones Provice.

Micrurus frontalis diana new subspecies

Holotype: FMNH No. 159889, a male from the vicinity of Santiago, Provincia Chiquiticos, Departamento Santa Cruz, Bolivia, 700 meters, collected by Roy F. Steinbach, April 7-20, 1973.

Paratypes: FMNH Nos. 1958864 and 195886, males, 195899, a female, and AMNH No. 120600, a male, all from the type locality collected by Roy F. Steinbach between March 1 and June 5, 1973.

Diagnosis: A *Micrurus frontalis* that differs from other subspecies in having the first black band of the first triad fused with the black coloration of the parietals. The only other subspecies in which this condition occurs occasionally is *M. f. frontalis* from which the new subspecies differs in having the red bands immaculate; *M. f. frontalis* has black tips on the red scales.

Description of the holotype: Rostral wider than high, visible from above; prefrontals about one and two thirds longer than internasals; frontal slightly longer than its distance from snout and only a little shorter than parietals; 1+1 temporals, a large posttemporal, reaching beyond tips of parietals. The holotype has 215 ventrals and 22 subcaudals, five of which are undivided.

The snout up to the frontal, supraoculars and postoculars is creamy yellow with the individual plates outlined by irregular black borders. The parietals, the posterior part of the frontal and supraoculars are black. On both sides of the parietals the head is red, including the last supralabials. There is a large black spot below the orbit, covering the upper part of the third and fourth supralabials. On the suture between the parietals is a narrow greyish white line. The black parietal coloration fuses with the first black band of the first triad. Inferiorly, the mental, the first three infralabials and the anterior pair of chin shields are creamy yellow, the rest of the head is red to the tips of the posterior pair of chin shields. A narrow black line runs between the anterior pair of chin shields.

There are nine complete black triads on the body with the black bands of approximately the same length, covering about three to four dorsals. The white bands are a little longer than the black bands and have small outline-type black tips. Ventrally, the black bands are irregular and the central bands of a triad are partially invaded by irregular whitish blotches that extend approximately along the midventral line. Most of the white bands have irregular larger black spots producing an impression of a feebly marked accessory black band. The red bands are seven to nine ventrals and dorsals long, without black tips. There are one and two thirds black triads on the tail.

The holotype has partially everted hemipenes. Each organ is bifurcated, approaching bilobed condition, with the *sulcus spermaticus* bifurcated. Except for the length of the first subcaudal, the organ is covered by fairly uniform size spines. A weak semicapitate condition is suggested by a line around the second subcaudal where the regular larger spines begin. The hemipenis *in situ* is about seven to eight subcaudals long.

The holotype has an overall length of 998 mm. The tail comprises 54 mm giving the ratio of tail length to total length of 0.0541.

Description of paratypes: In most characteristics the paratypes are similar to the holotype. There is variation in the amount and intensity of black outlining of the snout plates and of accessory black spots on the white bands. A constant feature is the whitish interparietal line. The black tips on the white scales as well as the larger irregular spots vary in size and intensity. The red bands are immaculate, except the FMNH No. 195864 which has one black scale in the center on the mid-dorsal line of most of the red bands. Ventrally, the outer black bands of triads are usually solid black, not invaded by irregular greyish white as in the holotype.

The males have 217 to 224 and the only female has 224 ventrals. The subcaudals range from 22 to 26 in males and are 20 in the only female. All males have some undivided subcaudals (4-11). All specimens except one have 9 body triads; FMNH No. 195864 has 10. On the tail, both sexes have one and one third to one two thirds of triads.

Remarks: This new subspecies has been found only in the Serranía de Santiago, an isolated mountain "island" surrounded by swampy lowlands. In the Serranía de San José de Chiquitos, about 160 km west of Santiago, *M. f. pyrrhocryptus* has been found.

This brilliantly colored and beautiful coral snake is dedicated to Diana, the goddess of forests, animals and the moon who should be adored and invoked to protect the endangered nature, particularly animals.

Micrurus frontalis multicoloratus Amaral

Micrurus lemniscatus multicoloratus Amaral, 1944, Pap. Avul. Dept. Zool. São Paulo, 5:91. (Type locality: Teixeira Soares, Paraná, Brazil).

Distribution: Probably from southern São Paulo to northern Rio Grande do Sul, Brazil.

Notes: Apparently, this is a valid subspecies that has wide zones of intergradation that still have to be defined. It intergrades with *M. f. frontalis* in São Paulo and with *M. f. altirostris* in Rio Grande do Sul.

Micrurus frontalis pyrrhocryptus (Cope)

Elaps pyrrhocryptus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 1862:347. (Type locality: Vermejo River, Argentine Choco).

Elaps simonsii Boulenger, 1902, Ann. Mag. Nat. Hist. (7)9:338. (Type locality: Cruz del Eje, Córdoba, Argentina).

Micrurus frontalis tricolor Hoge

Micrurus tricolor Hoge, 1956, Mem. Inst. Butantan, 27:67, figs. 1-4, 6. (Type locality: Garandazal, Mato Grosso, Brazil).

Distribution: Southeastern Mato Grosso, Brazil and adjacent Paraguay.

Notes: Further studies have revealed that the southeastern Mato Grosso population of *M. frontalis* represents a subspecific entity for which *M. tricolor* Hoge is available. It has a higher number of black triads than *M. f. pyrrhocryptus* (10 to 11 in males and 8 to 10 in females as compared to 5 to 8 for both sexes of *M. f. pyrrhocryptus*) with which it has been confused in the past.

Micrurus frontifasciatus (Werner)

Elaps frontifasciatus Werner, 1927, Sitz. Akad. Wiss. Vienna, 135:250. (Type locality: Bolivia).

Distribution: Eastern Andean slopes in Bolivia.

Notes: Apparently, this species is sympatric with *M. l. helleri* in Bolivia with which it probably forms a Mullerian mimicry system.

Micrurus fulvius fulvius (Linnaeus)

Coluber fulvius Linnaeus, 1766 (1766-1767), Syst. Nat., Ed. XII:381. (Type locality: Carolina, restricted to Charleston, South Carolina, United States by Schmidt, 1953).

Micrurus fulvius barbouri Schmidt, 1928, Bull. Antiven. Inst. Amer., 2:64. (Type locality: Paradise Key, Dade County, Florida, United States).

Distribution: Southeastern North Carolina to southern tip of Florida and the Gulf coastal plain to Mississippi, United States.

Micrurus fulvius fitzingeri (Jan)

Elaps fitzingeri Jan, 1858, Rev. Mag. Zool., (2)10:521. (Type locality: Mexico).

Distribution: Mexican plateau in Guanajuato and Querétaro to Morelos; probably also in Zacatecas, Aguascalientes and southern Coahuila, Mexico.

Notes: This subspecies intergrades with *M. f. tenere* in central Coahuila, and with *M. f. microgalbineus* along the southern border between Hidalgo and Querétaro, Mexico.

Micrurus fulvius maculatus Roze

Micrurus fulvius maculatus Roze, 1967, Amer. Mus. Novitates, 2287:27, fig. 10. (Type locality: Tampico, Tamaulipas, Mexico).

Distribution: Around Tampico, Tamaulipas, Mexico.

Micrurus fulvius microgalbineus Brown and Smith

Micrurus fitzingeri microgalbineus Brown and Smith, 1942, Proc. Biol. Soc. Washington, 55:63. (Type locality: Seven kilometers south of Antiguo Morelos, Tamaulipas, Mexico).

Distribution: Southwestern Tamaulipas, central and eastern San Luis Potosi to central Guanajuato, Mexico.

Notes: It intergrades with *M. f. tenere* in central Tamaulipas, Mexico.

Micrurus fulvius tenere (Baird and Girard)

Elaps tenere Baird and Girard, 1853, Cat. North Amer. Rept., 1:22, 156. (Type locality: San Pedro of Río Grande and New Braunfels, Texas, United States, restricted to the second locality by Smith and Taylor, 1950).

Elaps tristis Baird and Girard, 1853, Cat. North Amer. Rept., 1:23. (Type locality: Kemper County, Mississippi; Río Grande, west of San Antonio, Texas).

Distribution: West of the Mississippi River from Louisiana, Arkansas, and Texas to northern Coahuila, Nuevo León, and Tamaulipas, Mexico.

Micrurus hemprichii hemprichii (Jan)

Elaps hemprichii Jan, 1858, Rev. Mag. Zool. (2)10:523. Type locality: Colombia).

Distribution: Eastern Colombia and southern Venezuela to the Guyanas.

Micrurus hemprichii ortonii Schmidt

Micrurus hemprichii ortonii Schmidt, 1953, Fieldiana, Zool., 34:166. (Type locality: Pebas, Peru).

Distribution: Amazonian slopes of Colombia, Ecuador and Peru, also recorded from Alto Amazonas and Pará, Brazil.

Micrurus hippocrepis (Peters)

Elaps hippocrepis Peters, 1862, Monatsber. Akad. Wiss. Berlin, 1861:925. (Type locality: Santo Tomás (= Puerto Matías de Galvez), Guatemala).

Distribution: Caribbean lowlands of Belize and Guatemala.

Micrurus ibiboboca (Merrem)

Elaps ibiboboca Merrem, 1820, Tentamen Syst. Amphibiorum: 142. (Type locality: Brazil).



Elaps marcgravii Wied, 1820, Nova Acta Leop.-Carol., 10:109. (Type locality: Brazil, specified as mouth of Bio Belmonte (Bahia, Brazil) by Wied, 1825).

Distribution: Eastern Brazil.

Micrurus isozonus (Cope)

E(laps) isozonus Cope, 1860, Proc. Acad. Nat. Sci. Philadelphia, 1860: 73. (Type locality: South America, restricted to Caracas, Venezuela by Roze, 1955).

Elaps omissus Boulenger, 1920, Ann. Mag. Nat. Hist., (9)6:109. (Type locality: Venezuela).

Distribution: Northern and central Venezuela to Intendencia Meta, Colombia.

Micrurus karlschmidti Hoge and Romano

Leptomicru(ru)s schmidti Hoge and Romano, 1966, Mem. Inst. Butantan, 32:1, fig. 2. (Type locality: Tapurucuara, Amazonas, Brazil).

Micrurus karlschmidti Romano, 1972, Mem. Inst. Butantan, 35:111 (New name for *L. schmidti*, preoccupied by *M. schmidti* Dunn, 1940).

Distribution: Region of Rio Negro, Amazonas, Brazil.

Micrurus langsdorffi langsdorffi Wagler

Micrurus Lagsdorffi Wagler, 1824, in Spix, Sp. Nov. Serp. Bras.; 10, pl. 2, fig. 2. (Type locality: Rio Japurá, Amazonas, Brazil).

Elaps imperator (Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 1868: 110. (Type locality: Napo and Marañón, Peru).

Elaps batesi Günther, 1868, Ann. Mag. Nat. Hist., (4)1:428, pl. 17-1. (Type locality: Pebas, Peru).

Micrurus mimosus Amaral, 1935, Mem. Inst. Butantan, 9:221, fig. 6. (Type locality: Río Putumayo, Colombia).

Distribution: Upper Amazonian region from southern Colombia to northern Peru, including northwestern Brazil and adjacent Ecuador.

Notes: It intergrades with *M. l. ornatissimus* in northern Ecuador, near Colombian border.

Micrurus langsdorffi ornatissimus (Jan)

Elaps ornatissimus Jan, 1858, Rev. Mag. Zool., (2)10:521. (Type locality: Mexico, in error).

Elaps buckleyi Boulenger, 1896, Cat. Sn. Brit. Mus., 3:416, pl. 22-1. (Type locality: Canelos, Ecuador and Pará, Brazil).

Distribution: Amazonian slopes in eastern Ecuador and northern Peru.

Micrurus laticollaris laticollaris (Peters)

Elaps marcgravii var. *laticollaris* Peters, 1869, Monatsber. Akad. Wiss. Berlin, 1869:877.

Distributions Balsas River basin in Michoacán, Guerrero, Puebla and Morelos, Mexico.

Micrurus laticollaris maculirostris Roze

Micrurus laticollaris maculirostris Roze, 1967, *Amer. Mus. Novitates*, 2287:31. (Type locality Vicinity of Colima, Colima, Mexico).

Distribution: Colima and southern Jalisco, Mexico.

Micrurus latifasciatus Schmidt

Micrurus latifasciatus Schmidt, 1933, *Zool. Ser. Field Mus. Nat. Hist.*, 20:35 (Type locality: Finca El Ciprés, Volcán Zunil, Suchitepequez, Guatemala)

Micrurus nuchalis Schmidt, 1933, *Zool. Ser. Field Mus. Nat. Hist.*, 20:35. (Type locality: Tapanatepec, Oaxaca, Mexico).

Distribution: Pacific side of Oaxaca and Chiapas, Mexico and southern Guatemala.

Notes: Additional specimens from Oaxaca have demonstrated that *M. nuchalis* can not be distinguished from this species.

Micrurus lemniscatus lemniscatus (Linnaeus)

Elaps lemniscatus Linnaeus, 1758, *Syst. Nat.*, Ed.X:224. (Type locality: Asia, in error).

Distribution: Northern parts of Guyana, Surinam and French Guiana to adjacent Brazil.

Micrurus lemniscatus carvalhoi Roze

Micrurus lemniscatus carvalhoi Roze, 1967, *Amer. Mus. Novitates*, 2287:33, fig. 11. (Type locality: Catanduva, São Paulo, Brazil).

Distribution: Northeastern and central Brazil to Paraná and Mato Grosso.

Micrurus lemniscatus diutius Burger

Micrurus lemniscatus diutius Burger, 1955, *Bol. Mus. Cien. Nat. Caracas*, 1:8 (Type locality: Tunapuna, Trinidad).

Distribution: Trinidad, eastern Venezuela, and central parts of Guyana, Surinam and French Guiana.

Micrurus lemniscatus helleri Schmidt and Schmidt

Micrurus helleri Schmidt and Schmidt, 1925, *Zool. Ser. Field Mus. Nat.* 12:129. (Type locality: Pozuzo, Huánuco, Peru).

Distribution: Northern Brazil, southern Venezuela and Colombia to Amazonian foothills of Ecuador, Peru ad Bolivia.

Micrurus limbatus Fraser

Micrurus limbatus Fraser, 1964, *Copeia*, 3570, fig. (Type locality: Southern slope of Volcán San Martín, 7 airline miles north of San Andrés Tuxtla, Veracruz, Mexico).

Micrurus margaritiferus Roze

Micrurus margaritiferus Roze, 1967, *Amer. Mus. Novitates*, 2287:35, fig. 12. (Type locality: Boca Río Santiago — Río Marañón, Peru)

Distribution: Amazonian side of Andes in central Peru.



Micrurus mertensi Schmidt

Micrurus mertensi Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., 20:192. (Type locality: Pacasmayo, Peru).

Distribution: Lowlands of southwestern Ecuador to central Peruvian coastal area.

Micrurus mipartitus mipartitus (Duméril, Bibron and Duméril)

Elaps mipartitus Duméril, Bibron and Duméril, 1854, Erp. Gen. 7:1220. (Type locality: Río Sucip or Senio (?=Senu), Columbia).

Elaps aequicinctus Werner, 1903, Zool. Anz., 26:249. (Type locality: unknown).

Distribution: Darién of Panama to Pacific lowlands of Colombia.

Micrurus mipartitus anomalus (Boulenger)

Elaps anomalus Boulenger, 1896, Cat. Sn. Brit. Mus., 3:417, pl. 22, fig. 2. (Type locality: Colombia).

Distributions Santa Marta mountains and Cordillera Oriental, east of Magdalena River, Colombia to Andes in western Venezuela.

Micrurus mipartitus decussatus (Duméril, Bibron and Duméril)

Elaps decussatus Duméril, Bibron and Duméril, 1854, Erp. Gén., 7:1221. (Type locality: Probably Colombia).

Elaps fraseri Boulenger, 1896, Cat. Sn. Brit. Mus., 3:432, pl. 22, fig. 3. (Type locality: West Ecuador).

Elaps mentalis Boulenger, 1896, Cat. Sn. Brit. Mus., 3:432, pl. 22, fig. 4. (Type locality: Pallatanga, Ecuador, and Cali, Colombia).

Elaps calamus Boulenger, 1902, Ann. Mag. Nat. Hist., (7)9:57. (Type locality: San Javier, northwestern Ecuador).

Elaps microps Boulenger, 1913, Proc. Zool. Soc. London, 1913:1036, pl. 108, fig. 2. (Type locality: Peña Lisa, Condoto, Chocó, Colombia).

Distribution: Western and central Andes and southern part of eastern Andes in Colombia and western Ecuador; possibly Peru.

Micrurus mipartitus semipartitus (Jan)

Elaps semipartitus Jan, Rev. Mag. Zool., (2)10:113. (Type locality: Cayenne, restricted to Caracas, Venezuela by Roze (1955)).

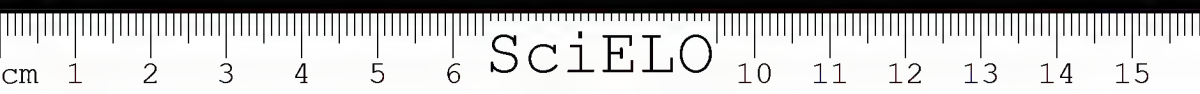
Distribution: Cordillera de la Costa in northern Venezuela.

Micrurus multifasciatus multifasciatus (Jan)

Elaps multifasciatus Jan, 1858, Rev. Mag. Zool., (2)10:521. (Type locality: Central America).

Distribution: Central Panama,

Notes: This Central American form apparently represents a species apart from *M. mipartitus* in which they were included previously. Both species are sympatric in Panama. As a rule, *M. multifasciatus* ssp. has



black-red body bands in life while *M. mipartitus* ssp. has black-white (yellow) body bands. In occasional specimens of *M. multifasciatus* ssp. the red bands might be pale pink or nearly white.

Micrurus multifasciatus hertwigi (Werner)

Elaps hertwigi Werner, 1897, Sitz. Akad. Wiss. Munich, 27:354. (Type locality: Central America).

Distribution: Caribbean slopes of Nicaragua, Costa Rica and Panama.

Micrurus multiscutatus Rendahl and Vestergren

Micrurus mipartitus multiscutatus Rendahl and Vestergren, 1940, Ark. for Zool., 33A(1):9, fig. 3. (Type locality: El Tambo, Cauca, Colombia).

Distribution: Cordillera Occidental of the Andes in Cauca, Colombia).

Notes: Additional specimen from Quebrada Guanguí, Saija drainage, Cauca, Colombia (AMNH No. 109781) collected by Charles Myers confirmed the validity of this species. In a living specimen, the snake has single black-red body bands whereas *M. mipartitus decussatus*, found in the same region, has black-white body bands.

Micrurus narducci (Jan)

Elaps narducci Jan, 1863, Arch. Zool. Anat. Fisiol., 21(2):222. (Type locality: Bolivia).

Elaps scutiventris Cope, 1869, Proc. Amer. Philos. Soc., 11:156. (Type locality: Pebas on the Amazon, Ecuador).

Elaps melanotus Peters, 1881, Sitzungsber. Ges. Naturf. Freunde, Berlin, 1881:51. (Type locality: Sarayacú, Ecuador).

Distribution: Amazonian slopes of the Andes in southern Colombia, Ecuador, Peru and Bolivia.

Micrurus nigrocinctus nigrocinctus (Girard)

Elaps nigrocinctus Girard, 1854, Proc. Acad. Nat. Sci. Philadelphia, 1854:226. (Type locality: Taboga Island, Bay of Panama).

Elaps melanocephalus Hallowell, 1860, Proc. Acad. Nat. Sci. Philadelphia, 1860:226. (Type locality: Ometepe, Nicaragua).

Micrurus pachecoi Taylor, 1951, Univ. Kansas Sci. Bull., 34:165, pl. 22, fig. 6. (Type locality: Guanacaste, Costa Rica).

Distribution: Pacific side of Nicaragua, Costa Rica and Panama to adjacent Colombia.

Notes: *M. nigrocinctus* is a complex assemblage of Central American coral snakes with broad areas of intergradation and isolated populations with unique features. Savage and Vial (1974) and Savage (1980) disregarded the subspecific subdivisions even though striking morphological differences have been found, especially in coloration. Recent findings of chromosomal differences between subspecies in Costa Rica, *M. n. nigro-*

cinctus and *M. n. mosquitensis* by Gutiérrez and Bolaños (1979 and 1981) and of venoms, have confirmed the subspecific validity of several morphologically recognizable units. Whereas the present arrangement and distribution of the subspecies of *M. nigrocinctus* represents only a partial picture of the complex group, lumping all subspecies disregards the biological reality of subspecies.

An analysis of the variation of populations from the Pacific side of Costa Rica and Nicaragua (Savage and Vial, 1974) indicates that *M. n. melanocephalus* cannot be reasonably recognized as a distinct subspecies. Whereas some features such as a narrow white parietal band is present in many but not all specimens from Costa Rica and Nicaragua, it is not a constant feature and the differences in ventral counts are somewhat overlapping with the population from Panama.

Micrurus nigrocinctus babaspul Roze

Micrurus nigrocinctus babaspul Roze, Amer. Mus. Novitates, 2287:38, fig. 13. (Type locality: Little Hill, Great Cord Island (Isla del Maíz Grande), in the Caribbean Sea, about 55 kilometers east-northeast of Bluefields, Nicaragua).

Distribution: Corn and Great Cord Islands, Nicaragua.

Micrurus nigrocinctus coinbensis Schmidt

Micrurus nigrocinctus coinbensis Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., 20:209. (Type locality: Coiba Island, Panama).

Distribution: Coiba Island, Panama.

Micrurus nigrocinctus divaricatus (Hallowell)

Elaps divaricatus Hallowell, 1855, Journ. Acad. Nat. Sci. Philadelphia, (2)3:36. (Type locality: Honduras).

Distribution: Northern and central Honduras and Belize.

Notes: This is an extremely variable subspecies (Wilson and Meyer, 1972) with broad areas of intergradation with *M. n. mosquitensis* in northeastern and northern Nicaragua and with *M. n. zunilensis* in eastern Guatemala and southwestern Honduras.

Micrurus nigrocinctus mosquitensis Schmidt

Micrurus nigrocinctus mosquitensis Schmidt, 1933, Zool. Ser. Field Mus. Nat. Hist., 20:33. (Type locality: Limon, Costa Rica).

Distribution: Atlantic slopes of eastern and southern Nicaragua, Costa Rica to northwestern Panama.

Micrurus nigrocinctus ruatanus (Günther)

Elaps ruatanus Günther, 1895, Biol. Centr. Amer., Rept.:185, pl. 57b.

Distribution: Roatán Island of Honduras.

Notes: Whereas no intergradation is known (Wilson and Meyer, 1972), apparently, this subspecies is related to *M. nigrocinctus*. Some specimens of *M. n. divaricatus* from Honduras mainland approach the

high number of black bands found in the population of Isla Roatán. It seems the evolutionary rate of speciation is faster in the island population a known phenomenon in evolutionary biology — for which *M. n. ruatanus* might serve as a classic example. Is *ruatanus* already a species or not is an open question due to its insular distribution.

Micrurus nigrocinctus zunilensis Schmidt

Micrurus nigrocinctus zunilensis Schmidt, 1932, Proc. Calif. Acad. Sci., (4)20:266. (Type locality: Finca El Cipres, lower slopes of Volcan Zuñil, Suchitepequez, Guatemala).

Micrurus nigrocinctus wagneri Mertens, 1941, Senckenbergiana, 23:216. Type locality: Finca Germania, Sierra Madre, Chiapas, Mexico, 400-1300 m.).

Micrurus nigrocinctus ovandoensis Schmidt and Smith, 1943, Zool. Ser. Field Mus. Nat. Hist., 29:26. (Type locality: Salto de Agua, Mount Ovando, about 15 mi northeast of Escuintla, Chiapas, Mexico).

Distribution: Pacific slopes of Chiapas, Mexico, southern Guatemala to El Salvador and southern Honduras).

Micrurus peruvianus Schmidt

Micrurus peruvianus Schmidt, 1936, Zool. Ser. Field Mus. Nat. Hist., 20:193. (Type locality: Perico, Departamento de Cajamarca, Peru)

Distribution: Andes of northeastern Peru.

Notes: The mountains of Cajamarca, Peru have several populations of coral snakes that might represent more than one endemic species. Considerably more material is needed for their correct interpretation.

Micrurus petersi Roze

Micrurus steindachneri petersi Roze, 1967, Amer. Mus. Novitates, 2287: 45, fig. 16. (Type locality: One mile south of Plan de Milagro, on the trail to Pan de Azúcar, Morona-Santiago Province, Ecuador, 5600 feet.

Distribution: Eastern slopes of Andes of Ecuador.

Notes: An additional specimen from Macas, Ecuador (MCZ No. 100950) suggests that this species is sympatric with *M. s. steindachneri* but has distinctive characteristics. A species status is assigned to this endemic Ecuadorian form.

Micrurus proximans Smith and Chrapliwy

Micrurus diastema proximans Smith and Chrapliwy, 1958, Herpetologica, 13(4):270. (Type locality: Four miles north of San Blas, Nayarit, Mexico).

Distribution: Nayarit, Mexico.

Micrurus psyches psyches (Daudin)

Vipera psyches Daudin, 1803, Hist. Nat. Rept., 8:320, pl. 100, fig. 1. (Type locality: Surinam).

Distribution: Extreme southern part of Colombia, eastern and southern Venezuela and the Guianas.

Micrurus psyches circinalis (Duméril, Bibron and Duméril)

Elaps circinalis Duméril, Bibron and Duméril, 1854, *Erp. Gén.*, 7:1210. (Type locality: Martinique, in error).

Distribution: Trinidad an adjacent mainland of Venezuela.

Micrurus psyches donosoi Hoge, Cordeiro and Romano

Micrurus donosoi Hoge, Cordeiro and Romano, 1976, *Ciência e Cultura* (Supl.), 28(7):417. (Type locality: Mineração Serra do Sul Ltda., 60 km north of São Félix do Xingu, Long. 51°55' W, Lat. 6°10'S, Para, Brazil).

Distribution: Known only from the type locality in Pará, Brazil.

Micrurus psyches medemi Roze

Micrurus psyches medemi Roze, 1967, *Amer. Mus. Novitates*, 2287:41, fig. 14. (Type locality: Villavicencio, Meta, Colombia).

Distribution: Vicinity of Villavicencio, Meta, Colombia.

Micrurus psyches paraensis Cunha and Nascimento

Micrurus psiches (sic!) *paraensis* Cunha and Nascimento, 1973, *Mus. Goeldi Ano Sesqui.*, Publ. Avuls., 20:275, figs. 1-2. (Type locality: Icoaraci, Belém, Pará (Brazil)).

Distribution: Around Belém, Pará, Brazil.

Micrurus putumayensis Lancini

Micrurus schmidti Lancini, 1962, *Publ. Ocas. Mus. Cien. Nat. Caracas, Zool.*, 2:1, fig. 1. (Type locality: Puerto Socorro, 270 km northeast of Iquitos, Río Putumayo, Depto. Loreto, Peru).

Micrurus putumayensis Lancini, 1963, (New name for *M. schmidti*, preoccupied by *M. schmidti* Dunn, 1940), *Publ. Ocas. Mus. Cien. Nat. Caracas, Zool.*, 3:1.

Distribution: Amazon basin in northeastern Peru and eastern Brazil; probably also southern tip of Colombia.

Micrurus sangilensis Niceforo Maria

Micrurus ecuadorianus sangilensis Nicéforo María, 1942, *Rev. Acad. Colomb. Cien. Exact. Fis. Nat.*, 5.98, pl. 3, fig. 10. (Type locality: San Gil, Santander, Colombia).

Distribution: Between Cordillera Central and Oriental in northern Colombia.

Notes: Apparently, this form is not related to *M. bocourti* with which it has been associated in the past.

Micrurus spixii spixii Wagler

Micrurus spixii Wagler, 1824, is Spix, *Sp. Nov. Serp. Bras.* :48, pl. 18. (Type locality: Rio Solimões, Brazil).

Elaps ehrhardti Müller, 1926, *Zool. Anz.*, 7/8:198. (Type locality: Manacapurú, Rio Solimões, Brazil).

Distribution: Middle Amazonian region of Brazil.

Micrurus spixii martiusi Schmidt

Micrurus spixii martiusi Schmidt, 1953, *Fieldiana, Zool.*, 34:175, figs. 33-34. (Type locality: Santarém, Pará, Brazil).

Distribution: Amazonian drainage of Pará and Mato Grosso, Brazil.

Micrurus spixii obscurus (Jan)

Elaps corallinus var. *obscura* Jan, 1872 in Jan and Sordelli, *Icon. Gén. Ophid.*, Livr. 41:pl. 6, fig. 3. (Type locality: Lima, corrected and restricted to eastern Peru by Schmidt and Walker, 1953, and further designated as Iquitos, Peru by Schmidt, 1953).

Elaps heterozonus Peters, 1881, *Sitz. Ges. Naturforsch. Freunde Berlin*, 1881:52. (Type locality: Sarayacú, Ecuador).

Distribution: Periphery of Amazon basin, from southern Venezuela and Colombia to southern Peru, also northern tip of Brazil.

Micrurus spixii princeps (Boulenger)

Elaps princeps Boulenger, 1905, *Ann. Mag. Nat. Hist.*, (7)15:456. (Type locality: Provincia Sara, Departamento Santa Cruz de la Sierra, Bolivia).

Distribution: Northwestern and central Bolivia

Micrurus spurelli (Boulenger)

Elaps spurelli Boulenger, 1914, *Proc. Zool. Soc. London*, 1914:817. (Type locality: Peña Lisa, Río Condoto, Colombia).

Micrurus nicefori Schmidt, 1955, *Fieldiana, Zool.*, 34:346, fig. 65. (Type locality: Villavicencio, Cundinamarca, Colombia).

Distributions Western and central Colombia.

Micrurus steindachneri steindachneri (Werner)

Elaps Steindachnei Werner, 1901, *Verh. Zool. Bot. Ges. Vienna*, 51:599. (Type locality: Ecuador).

Elaps fassli Werner, 1926, *Sitz. Math.-Naturwiss. Kl. Akad. Wiss. Wien*, 135(1):249. (Type locality: Colombia).

Distribution: Eastern slopes of Andes in Macas-Mendez region, southern Ecuador.

Micrurus steindachneri orcesi Roze

Micrurus steindachneri orcesi Roze, 1967, *Amer. Mus. Novitates*, 2287:43, fig. 15. (Type locality: Meta trail, Baños, Ecuador, 1200 m.)

Distribution: Higher elevations, from 1000 to 1800 m. in valley of Rio Pastaza, Pastaza Province, Ecuador.

Micrurus stewarti Barbour and Amaral

Micrurus stewarti Barbour and Amaral, 1928, Bull. Antivenin Inst. Amer., 1:100. (Type locality: Nombre de Dios, Sierra de la Bruja, Panama).

Micrurus schmidti Dunn, 1940, Proc. Acad. Nat. Sci. Philadelphia, 92: 119, pl. 2. Type locality: Valle de Antón, 50 mi west of Canal Zone, Panama, 2000 ft.).

Distribution: Intermediate elevations east and west of Canal Zone, Panama.

Micrurus stuarti Roze

Micrurus stuarti Roze, 1967, Amer. Mus. Novitates, 2287:47, fig. 17. (Type locality: Finca La Paz, San Marcos, Guatemala, 1345 m).

Distribution: San Marcos and Suchitepequez, Guatemala.

Micrurus surinamensis surinamensis (Cuvier)

Elaps surinamensis Cuvier, 1817, Le Règne Animal, 2.84. (Type locality: Surinam).

Distribution: Amazonian region in Colombia, Ecuador, Peru, Brazil, Bolivia and the Guianas.

Micrurus surinamensis nattereri Schmidt

Micrurus surinamensis nattereri Schmidt, 1952, Fieldiana, Zool., 34:27. (Type locality: Between Guaramoca and San Fernando, Venezuela).

Distribution: Upper Río Orinoco and Río Negro region of southern Venezuela and northern Brazil.

Micrurus tschudii tschudii (Jan)

Elaps tschudii Jan, 1858, Rev. Mag. Zool., (2)10:524. (Type locality: Peru).

Distribution: Pacific slopes from southern Ecuador to southern Peru and probably northwestern Bolivia.

Micrurus tschudii olssoni Schmidt and Schmidt

Micrurus olssoni Schmidt and Schmidt, 1925, Zool. Ser. Field Mus. Nat. Hist., 12:130, pl. 11. (Type locality: Negritos, Piura, Peru).

Distribution: Pacific slopes from southern Ecuador to northwestern Peru.

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SOBRE A DISTRIBUIÇÃO GEOGRÁFICA DOS GÊNEROS DA SUBFAMÍLIA THERAPHOSINAE THORELL, 1870 NO BRASIL (ARANEAE, THERAPHOSIDAE)

Sylvia LUCAS *

RESUMO: A subfamília THERAPHOSINAE Thorell, 1870 abrange atualmente 11 gêneros e cerca de 90 espécies, a grande maioria ocorrendo na América do Sul e principalmente no Brasil. Neste trabalho são apresentados mapas de distribuição geográfica dos gêneros que ocorrem no Brasil, baseados em material recebido pela Seção de Artrópodes Peçonhentos do Instituto Butantan e em exemplares depositados nas coleções da mesma seção. Verificou-se que a grande maioria dos exemplares recebidos pertencem aos gêneros *Pamphobeteus* Pocock, 1901, *Acanthoscurria* Ausserer, 1871 e *Lasiadora* C. Koch, 1850. As legendas dos mapas mostram as quantidades de material recebido. Quanto ao gênero *Megaphoboema* Pocock, 1901 não houve registro de recebimento e não há material depositado nas coleções, procedente do Brasil. É questionada a ocorrência do gênero *Phormictopus* Pocock, 1901 no Brasil, tendo-se examinado o tipo de *P. pheopygus* Mello Leitão, 1923 e verificado tratar-se de uma *Acanthoscurria gomesiana* Mello Leitão, 1923. Os tipos de *P. multicuspidatus* Mello Leitão 1929, *P. ribeiroi* Mello Leitão, 1923 e *P. brasiliensis* Strand, 1907 teriam que ser revistos, afim de constatar se realmente pertencem ao gênero, uma vez que as descrições são incompletas. Após a revisão do tipo, constatou-se que a única espécie descrita como ocorrendo no Brasil, do gênero *Sericopelma* Ausserer, 1875, *S. fallax* Mello Leitão, 1923, não pertence ao mesmo e o gênero, portanto, não foi incluído nos mapas apresentados.

PALAVRAS CHAVE: Subfamília THERAPHOSINAE; distribuição geográfica dos gêneros no Brasil; ARANEAE; THERAPHOSIDAE, THERAPHOSINAE.

INTRODUÇÃO

A subfamília THERAPHOSINAE Thorell, 1870 abrange 11 gêneros e cerca de 90 espécies, ocorrendo a maioria na América do Sul e principalmente no Brasil.

Muitas espécies são conhecidas apenas através do material tipo, às vezes, um único exemplar e as descrições são sumárias, omitindo caracte-

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teres importantes e os locais de coleta são duvidosos, tornando difícil a correta identificação dos gêneros e espécies.

Entre os pesquisadores que contribuíram para o melhor conhecimento desta subfamília devemos citar, entre outros, Mello Leitão (6), que em 1923 redescreveu várias espécies, descreveu espécies novas e citou muitas vezes não só a localidade de coleta, bem como, a distribuição geográfica da espécie em questão. Também Vellard (7) em 1936, estudando o veneno de diversas espécies pertencentes ao gênero *Acanthoscurria* Ausserer, 1871, *Phormictopus* Pocock, 1901, e *Pamphobeteus* Pocock, 1901, descreveu hábitos e citou a distribuição geográfica de algumas espécies. Ainda Bücherl (1, 2, 3) em diversos trabalhos e também Gerschman de Pikelin e Schiapelli (4), em 1967, fizeram um estudo comparativo dos gêneros *Theraphosa* Walcknaer, 1805, *Lasiadora* e *Sericopelma* Ausserer, 1875 e apresentaram mapas de distribuição geográfica dos três gêneros.

O Instituto Butantan possui em seu acervo uma coleção de ORTHOGNATHA constando de mais de 4.000 exemplares, sendo esta constantemente ampliada através da anexação de material recebido das mais diversas localidades.

Neste trabalho fizemos um levantamento a nível genérico do material recebido, pertencente à subfamília THERAPHOSINAE e apresentamos mapas de procedências.

MATERIAL E MÉTODO

A Seção de Artrópodes Peçonhentos do Instituto Butantan atende, anualmente, mais de 2.000 pessoas que procuram a Seção, trazendo aracnídeos coletados nos arredores de suas residências, em sítios, fazendas etc. Na Seção são informados sobre a periculosidade do animal em questão, métodos de erradicá-lo, quando necessário, orientação sobre como prevenir o acidente e demais informações úteis.

Os aracnídeos são registrados em livro, recebendo um número de referência, de acordo com a ordem de entrada. Constam nos livros, iniciados em 1967, o nome e o endereço postal do fornecedor, a data do recebimento, o local de coleta e a identificação do animal a nível genérico.

A Seção recebeu, num período de cinco anos (1976 a 1980) 3.276 exemplares de aranhas caranguejeiras e atendeu 11.500 fornecedores. Excluindo-se os aracnídeos de interesse médico, gêneros *Phoneutria*, *Loxosceles* e *Lycosa*, figuram as aranhas caranguejeiras em primeiro lugar, por ordem de recebimento, podendo-se atribuir isto ao fato de que devido ao seu tamanho, serem consideradas perigosas e portanto temida pela população.

Fizemos um levantamento do material pertencente à subfamília THERAPHOSINAE, recebido durante o período de 1976 a 1980, inclusive. As procedências foram assinaladas em mapas. Para os gêneros *Pamphobeteus* e *Acanthoscurria* as localidades assinaladas no Estado de São Paulo são muitas e por isso constam em mapas separados. Nas legendas dos mapas estão assinaladas as quantidades de material recebido de cada gênero, por localidade. Não foram consideradas as procedências duvidosas, isto é, aranhas que vieram em transporte de madeira etc.

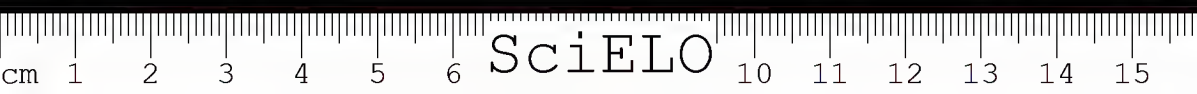




Fig. 1. Gênero *Acanthoscurria*: mapa do Estado de São Paulo assinalando as procedências e as quantidades de material recebido.

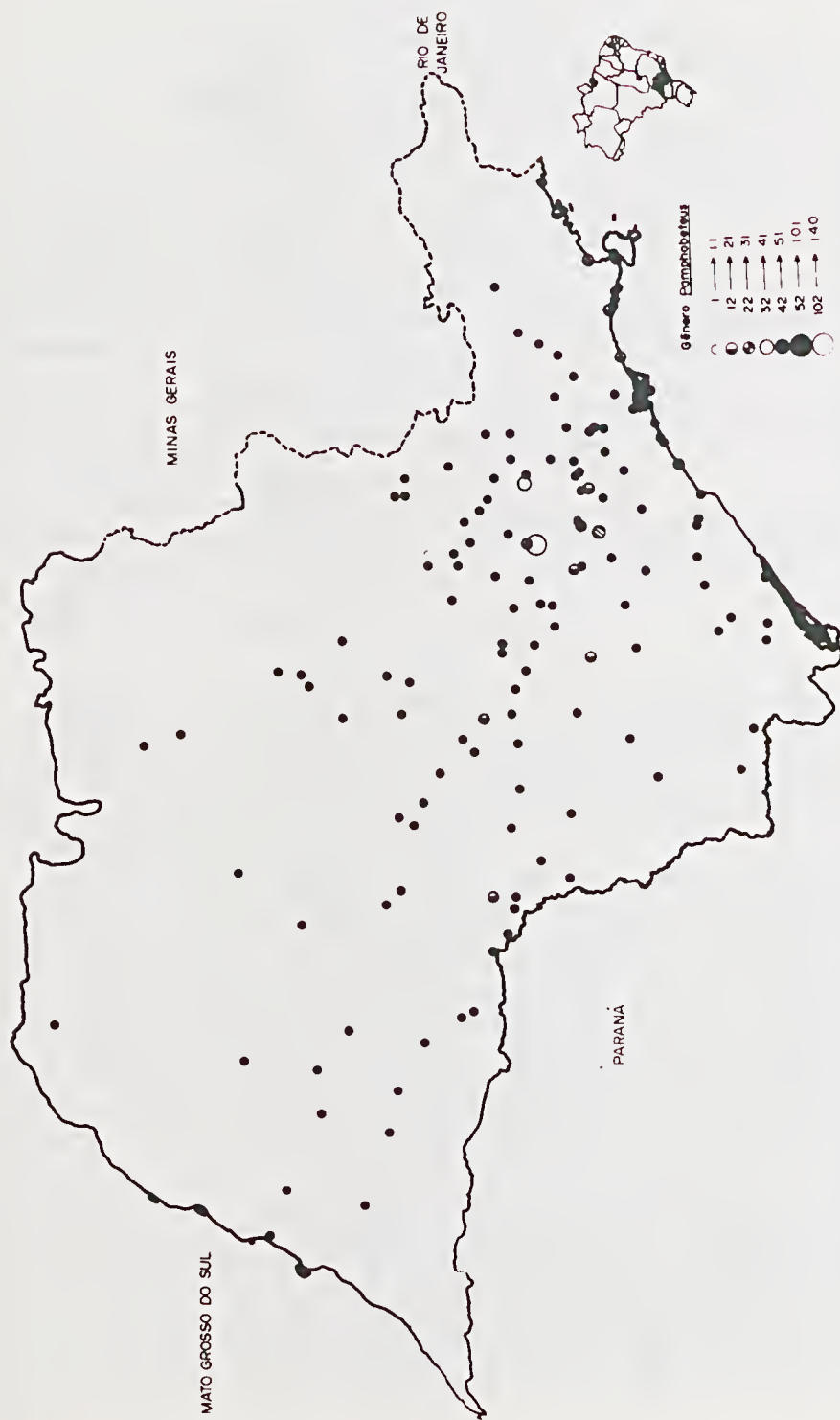


Fig. 2. Gênero *Pamphobeteus*: mapa do Estado de São Paulo assinalando as procedências e as quantidades de material recebido.

Quanto aos gêneros *Trasyphoberus* Simon, 1903, *Xenesthis* Simon, 1891, *Eupalaestrus* Pocock, 1901 e *Theraphosa* Walckenaer, 1805, cujo número de exemplares recebidos é muito pequeno, consideramos todas as procedências que constam nos registros da coleção e foi feito apenas um mapa geral.

O GÊNERO *Acanthoscurria* AUSSERER, 1871

Há cerca de 32 espécies descritas das quais 22 para o Brasil.

Durante o período de cinco anos recebemos 766 exemplares. *Acanthoscurria gomesiana* Mello Leitão, 1923 é a espécie recebida com maior frequência, principalmente dos arredores da capital de São Paulo.

Recebemos material das seguintes procedências:

BAHIA: Feira de Santana, Irerê.

DISTRITO FEDERAL: Brasília.

GOIÁS: Cristalina, Crixás, Itumbiara, Monzolândia, Paracatu, Distrito Federal.

MATO GROSSO: Aripuanã, Barra do Garça, Cáceres, Nobres.

MATO GROSSO DO SUL: Campo Grande, Coxim, Miranda.

MINAS GERAIS: Alterosa, Belo Horizonte, Caxambu, Cristiano Otoni, Estiva, Extrema, Guaranésia, Iturama, Jacuí, Juiz de Fora, Liberdade, Monte Verde, Poços de Caldas, Rio Acima, Sacramento, Uberaba, Uberlândia, Vargem da Palma.

PARÁ: Belém, Santarém, Marabá.

PIAUI: Avelino Lopes, São Raimundo Nonato, Teresina.

RIO DE JANEIRO: Barra Bonita, Vargem Grande.

SÃO PAULO: Adamantina, Águas de Lindóia, Água Vermelha, Atibaia, Americana, Amparo, Angatuba, Araçoiaba da Serra, Araraquara, Assis, Bariri, Barueri, Bauru, Bebedouro, Bela Aliança, Bocaina, Boituva, Bragança Paulista, Brotas, Cabreúva, Caçapava, Caiabu, Caiéiras, Cajamar, Camanducaia do Alto, Campinas, Campo Limpo Paulista, Cananéia, Caucaia do Alto, Colina, Cotia, Descalvado, Diadema, Embu, Embu-Guaçu, Espírito Santo do Pinhal, Ferraz de Vasconcelos, Flórida Paulista, Francisco Morato, Franco da Rocha, Fronteiras, Garça, Guarulhos, Ibiúna, Indaiatuba, Iracemápolis, Itaim, Itarará, Itatiba, Itirapina, Itu, Itupeva, Jacareí, Jaguariúna, Jandira, Jarinu, Jundiá, Juquiá, Juquitiba, Lindóia, Louveira, Mairinque, Mairiporã, Mailasque, Martinópolis, Matão, Miracatu, Mococa, Mogi das Cruzes, Mogi-Guaçu, Mogi-Mirim, Morungaba, Nazaré Paulista, Osasco, Osvaldo Cruz, Ourinhos, Paraibuna, Paranapiacaba, Paulínia, Piedade, Penápolis, Pinhal, Pinhalzinho, Piracaia, Pirapora do Bom Jesus, Pirassununga, Porangaba, Poá, Porto Feliz, Quitaúna, Rancharia, Registro, Rincão, Ribeirão Preto, Rio Claro, Sales de Oliveira, Salto, Santa Adélia, Santa Bárbara d'Oeste, Santa Gertrudes, Santana do Parnaíba, Serra Negra, São Bernardo do Campo, São Carlos, São João da Boa Vista, São João Novo, São Mateus, São Roque, Sumaré, Taboão da Serra, Tatuí, Tupã, Valinhos, Vargem Paulista, Votorantim.

O GÊNERO *Pamphobeteus* POCOCK, 1901

Em revisão do gênero, realizada por Bücherl (1, 2) em 1947 e em 1948, as 19 espécies descritas para o Brasil foram reduzidas a apenas 8.

Há dúvida porém quanto à correta identificação das espécies pertencentes ao gênero que ocorrem no Brasil. Em *P. nigricolor* (Ausserer, 1875), a dobradura do metatarso do palpo se dá entre as apófises tibiais, enquanto que em material depositado nas coleções do Instituto Butantan, identificado por Bücherl e em várias descrições de espécies novas de Mello Leitão, o metatarso dobra-se sobre a apófise externa. O caracter tem importância genérica havendo necessidade de mais estudos.

Procedências do material recebido:

MATO GROSSO: Alta Floresta, Aripuanã e Barra do Garça.

MATO GROSSO DO SUL: Campo Grande, Dourados, Nova Andradina, Ponta Porã.

MINAS GERAIS: Bom Jesus do Galho, Juiz de Fora, Poços de Caldas e Uberaba.

PARÁ: Belém, São José de Guamar.

PARANÁ: Arapongas, Apucarana, Cambará, Cambé, Castro, Curitiba, Foz de Iguaçu, Guarapuava, Jaguariaíva, Londrina e Rolândia.

PIAUI: Avelino Lopes, Santa Cruz.

RIO DE JANEIRO: Angra dos Reis, Pirai, Nova Friburgo e Parati.

RONDÔNIA

SANTA CATARINA: Capinzal e Joinville.

SÃO PAULO: Airosa Galvão, Agenor de Campos, Água Vermelha, Água de Santa Bárbara, Agudos, Americana, Américo Brasiliense, Amparo, Ana Dias, Angatuba, Apiaí, Araraquara, Arujá, Assis, Atibaia, Avaré, Barra do Sahi, Barra do Una, Barueri, Bertioga, Boa Esperança do Sul, Bofete, Boituva, Boracéia, Botucatu, Bragança Paulista, Brotas, Buri, Cachoeirinha, Caieiras, Camburi, Campinas, Campo Limpo, Cananéia, Cândido Mota, Caraguatatuba, Carapicuíba, Capivari, Caucaia, Cerqueira César, Cesário Lange, Colina, Conchas, Corumbataí, Cotia, Cubatão, Daldema, Dois Córregos, Dracena, Embu, Engenheiro Marsilac, Engenho, Fartura, Gália, Garça, Gavião Peixoto, Grajaú, Guararapes, Guararema, Guarujá, Guarulhos, Ibiúna, Iguape, Ilha Bela, Ilha Comprida, Ilha Porchat, Indaiatuba, Inúbia, Ipiaçu, Iporanga, Irapoã, Itai, Itanhaém, Itapeva, Itapevi, Itapetininga, Itaquera, Itariri, Itatiba, Itatinga, Itu, Jacaré, Jacupiranga, Jarinu, Jaú, Jundiá, Juqueí, Juquiá, Juititaba, Lençóis Paulista, Limeira, Lins, Lucélia, Mairinque, Martinópolis, Miracatu, Mogi das Cruzes, Mogi-Guaçu, Mogi-Mirim, Mongaguá, Nova Odessa, Osasco, Ourinhos, Panorama, Paraguaçu Paulista, Paranapiacaba, Pardinho, Pariqueira-Açu, Paulínia, Pedro de Toledo, Pereira, Peruíbe, Piedade, Pilar do Sul, Piraju, Piratininga, Porangaba, Porto Feliz, Praia Grande, Praia de Pernambuco, Pratânia, Registro, Rincão, Rio do Peixe, Rinópolis, Rio das Pedras, Salto Grande, São Sebastião, São José dos Campos, Santa Bárbara d'Oeste, Sorocaba, São Bernardo, São Miguel Arcanjo, São Manoel, Santo Anastácio, Santo André, Sumaré, São Vicente, Santa Cruz do Rio Pardo, Salto, São Caetano, São Roque, São Lourenço da Serra, São Carlos, Sete Barras, Taboão da Serra, Tapiraí, Tatuí, Taubaté, Tietê, Torrinha, Tupã, Uberaba Uirapuru, Valinhos, Várzea Paulista, Votorantim, Valinhos e Xavantes.

SERGIPE: Aracaju.



Fig. 3. Gênero *Acanthoscurria*: mapa do Brasil assinalando as procedências e as quantidades de material recebido.



Fig. 4. Gênero *Pamphobeteus*: mapa do Brasil assinalando as procedências e as quantidades de material recebido.

O GÊNERO *Lasiadora* C. L. Koch, 1851

Há 21 espécies descritas, a grande maioria ocorrendo no Brasil. A espécie *L. klugi* C. L. Koch, 1842, é trazida freqüentemente ao Instituto junto com transporte de madeira procedente do Nordeste.

Gerschman de Pikelin e Schiapelli identificaram, em 1967, como pertencente a este gênero, material procedente da Venezuela e sugeriram que o mesmo ocorra na região amazônica. Nas ilustrações que acompanham o trabalho podemos verificar que os exemplares identificados não pertencem ao gênero *Lasiadora*.

Recebemos material das seguintes procedências:

BAHIA: Barragem Pedra do Cavalo, Brumado, Coqueiros, Jequié, Morro do Chapéu, Nova Viçosa, Paulo Afonso.

ESPIRITO SANTO: Santa Teresa, Vitória.

GOIAS: Alvorada, Goiás, Itumbiara.

MATO GROSSO: Mato Grosso.

MINAS GERAIS: Belo Horizonte, Bom Jesus do Galho, Caratinga, Corinto, Furnas do Sul, Itaberaba, Juiz de Fora, Montes Claros, Taubim, Três Corações, Uberaba.

PIAUI: Avelino Lopes, Landri Sales, São Raimundo Nonato, Terezina.

RIO DE JANEIRO: Alberto Torres, Abrão, Angra dos Reis, Barra do Pirai, Campos, Mendes, Nova Friburgo, Parati, Rio de Janeiro, Teresópolis, Vassouras, Visconde de Mauá, Volta Redonda.

SÃO PAULO: Água Branca, Bela Vista, Campinas, Caçapava, Caraguatatuba, Casa Verde, Caxingui, Guararema, Iguape, Itanhaém, Jaboticabal, Jardim São Bento, Mongaguá, Monte Azul Paulista, Paraibuna, Praia Grande, Pindamonhangaba, Queluz, Registro, Santana, Sertãozinho, Santo André, São José do Barreiro, São José dos Campos, Sorocaba, Taubaté, Vale do Paraíba, Vila Jaraguá.

O GÊNERO *Eupalaestrus* Pocock, 1901

Há cinco espécies descritas, três para o Brasil. Nas coleções do Instituto Butantan há material recebido das seguintes localidades:

MATO GROSSO DO SUL: Agachi, Bonito, Campo Grande, Coxim, Nioaque, Palmeiras, Taunay.

PARANÁ: Guarapuava, Laranjeira do Sul, Ponta Grossa.

RIO GRANDE DO SUL: Pelotas.

SANTA CATARINA: Capinzal, Serra Alta.

SÃO PAULO: São José dos Campos.

O GÊNERO *Megaphoboema* Pocock, 1901

É um gênero monotípico, *M. robusta* (Ausserer, 1875), é de Bogotá, Colômbia.

Gerschmann e Schiapelli em 1979, viram o tipo: um macho, que pelo formato do bulbo copulador aproxima-se ao gênero *Sericopelma* Ausserer, 1875.

Não há registro deste gênero nas coleções do Instituto Butantan.



Fig. 5. Gênero *Lasiadora*: mapa dos Estados de São Paulo, Rio de Janeiro, Espírito Santo, Minas Gerais, Goiás e Piauí assinalando as procedências e as quantidades de material recebido.



Fig. 6. Gêneros *Trasyphoberus*, *Theraphora*, *Xenesthis*, *Eupalaestrus* e *Nhandu*: mapa do Brasil assinalando as procedências do material recebido.

O GÊNERO *Nhandu* Lucas, 1981

O gênero apresenta apenas uma espécie, *Nhandu carapoensis* procedente de Carapó, Mato Grosso do Sul.

Recebemos mais material pertencente ao gênero de: Campo Grande, Nioaque e Pedro Gomes, Mato Grosso do Sul.

O GÊNERO *Phormictopus* Pocock, 1901

Há 13 espécies descritas das Antilhas e da América do Sul.

Em 1923, Mello Leitão descreveu duas espécies do Brasil: *P. ribeiroi* de Mato Grosso e *P. pheopygus* de São Paulo, e em 1929, mais uma da Bahia, *P. multicuspidatus*.

Vellard, em 1936, estudou o veneno de *P. brasiliensis* Strand, 1907 e *P. pheopygus*, citando-as como ocorrendo no sul de Mato Grosso, noroeste de São Paulo, sul de Minas e Goiás. Identificou o gênero pela presença, nos machos, de dois esporões tibiais.

Gerschmann e Schiapelli, em 1979, citam ocorrência do gênero no Brasil, Cuba, Antilhas, Venezuela, Estados Unidos e também na Nicarágua.

Examinando o tipo de *P. pheopygus* e verificamos tratar-se de uma *Acanthoscurria gomesiana* Mello Leitão, 1923.

Não há registro de exemplares pertencentes ao gênero nas coleções do Instituto Butantan, apesar de ter sido recebido material das localidades citadas por Vellard. Há necessidade de um estudo dos tipos a fim de se verificar se de fato as demais espécies identificadas para o Brasil e talvez, América do Sul, pertencem ao gênero.

O GÊNERO *Sericopelma* Ausserer, 1875

Foram descritas três espécies, duas do Panamá uma no Brasil. Gerschmann de Pikelin e Schiapelli, em 1967, identificaram material do gênero coletado na Nicarágua.

Examinamos o tipo de *S. fallax* Mello Leitão, 1923, e constatamos não pertencer ao gênero. Nas coleções do Instituto Butantan não há material pertencente ao gênero.

O GÊNERO *Theraphosa* Walckenaer, 1805

É um gênero monotípico, a espécie *T. leblondii* (Latreille, 1804) foi coletada na região do Maroni, nas Guianas. Walckenaer afirmou ter recebido material pertencente a este gênero procedente do Pará, fato posto em dúvida por Mello Leitão e confirmado por nós.

Recebemos exemplares procedentes do Território do Amapá, da região da Serra do Navio e do Pará: Belém, Marabá, São Félix do Xingu, além de vários exemplares das Guianas Britânicas.

O GÊNERO *Trasyphoberus* Simon, 1903

O gênero é monotípico e a espécie *T. parvitarsis* Simon, 1903 foi descrita de Tefé, Amazonas. O gênero aproxima-se de *Acanthoscurria*.

Em trabalho no prelo, estabelecemos a sinonímia de *parvitarsis* com *ferina* Simon, 1892. Examinamos os tipos de ambas espécies, e verifica-



mos que os receptáculos seminais de *parvitaris* são idênticos aos de *ferina*. O tipo de *parvitaris* está em mau estado de conservação.

Nas coleções do Instituto Butantan há vários exemplares procedentes do Amazonas, Boca do Tefé, Humaitá, Manicore e Três Casas.

O GÊNERO *Xenesthis* Simon, 1891

O gênero apresenta três espécies descritas para a América Central, Colômbia e Venezuela. A espécie tipo é *X. immanis* (Ausserer, 1875) da América Central.

Nas coleções do Instituto Butantan há dois exemplares procedentes do Estado de Rondônia: Pimenta Bueno.

CONCLUSÕES

A Seção de Artrópodes Peçonhentos recebe anualmente, em maior número, as aranhas pertencentes à subordem ORTHOGNATHA, excluindo-se os gêneros da subordem LABIDOGNATHA de interesse médico, isto é, *Phoneutria*, *Lycosa* e *Loxosceles*.

Os gêneros da subfamília THERAPHOSINAE recebidos com maior frequência são *Pamphobeteus*, *Acanthoscurria* e *Lasiadora*.

No Estado de São Paulo ocorrem em maior abundância os gêneros *Pamphobeteus* e *Acanthoscurria*, sendo a espécie *A. gomesiana* a caranguejeira mais freqüentemente recebida dos arredores da capital.

A ocorrência do gênero *Phormictopus* no Brasil é por enquanto duvidosa, pois apesar de Vellard assinalar a ocorrência de duas espécies nos Estados de Mato Grosso, Minas Gerais, São Paulo e Goiás, não há material identificado como pertencente a este gênero, nas coleções do Instituto Butantan.

Não há registro de ocorrência dos gêneros *Megaphoboema* e *Serico-pelma* no Brasil e a espécie *S. fallax* não pertencente ao gênero.

AGRADECIMENTOS

O levantamento das localidades de recebimento do material e sua localização nos mapas foi realizado pela equipe da Seção de Artrópodes Peçonhentos constituída pelas assistentes biólogas Irene Knysak e Livia Zveibil e pelos estagiários Maria Cristina dos Santos, Miriam Costa e Ricardo Bottino.

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